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Fisheries and Marine Service

Pêches et Environnement Canada
Service des pêches et de la mer

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Index

An author–subject index and list of all publications issued during 1977 will be supplied in early 1978, and distributed free to all *Journal* recipients, including subscribers. Additional copies will be available through the Scientific Information and Publications Branch.

Index

Un index par sujet et auteur et une liste de toutes les publications parues en 1977 paraîtront au début de 1978 et seront distribués gratuitement à tous ceux qui reçoivent le *Journal*, ainsi qu'aux abonnés. On pourra se procurer des exemplaires supplémentaires à la Direction de l'information et des publications scientifiques.

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Announcement

In this issue we experiment with a form of miniprint for extensive tabular material (see p. 2257 and 2273). This consists of reducing the author's typed table to about one quarter of its original size. Those with good vision should be able to read the material directly; others may require a magnifying lens. By eliminating typesetting costs and saving 75% of the space used for normal printing, this format will allow us to publish data compilations that are essential for understanding some papers.

This experiment should not be construed as an invitation to submit lengthy tables of raw data. In most cases it is neither desirable nor feasible to reproduce untreated data in the primary literature where the function is to communicate the new knowledge resulting from analysis and interpretation. Raw data should be accommodated in data repositories or the report literature. However, occasionally we do receive a paper that cannot be understood properly without reference to a large data base. If the data are extensive, appropriate presentation is a problem. Tabular material is expensive to typeset and occupies much valuable space which would normally accommodate other papers. It has been suggested that essential data be produced as microfiche insertions in the *Journal*. However, miniprint is far less expensive and, even if a magnifying lens must be used, more convenient than microfiche.

We welcome comments from readers.

Avis

Nous expérimentons dans le présent numéro une forme de miniimpression de tableaux volumineux (voir p. 2257 et 2273) qui ont été réduits à un quart de leur grandeur originelle. Le lecteur qui a bonne vue devrait pouvoir lire le matériel directement; les autres auront à se servir d'une loupe. Ce format, en éliminant le coûts de composition et en économisant 75% de l'espace requis par une impression normale, nous permettra de publier des données essentielles à la compréhension de certains articles.

Il ne faudrait pas considérer cette expérience comme une invitation à soumettre de longs tableaux de données brutes. Dans la plupart des cas, il n'est ni désirable ni possible de reproduire des données brutes dans un périodique de fonds dont le rôle est de communiquer les connaissances nouvelles résultant de l'analyse et de l'interprétation. Les banques de données ou les séries de rapports sont là pour recevoir les données brutes. Cependant, il nous arrive parfois un article qui ne peut être très bien compris sans un assez grand nombre de données. La présentation appropriée d'un grand volume de données pose un problème. La composition de tableaux est dispendieuse et occupe un espace précieux qui devrait normalement être accordé à d'autres articles. On a suggéré de reproduire les données essentielles sur microfiches insérées dans le *Journal*. Cependant, la miniimpression est beaucoup moins dispendieuse et, même si l'on doit se servir d'une loupe, est plus commode que la microfiche.

Les commentaires de nos lecteurs seront les bienvenus.

Phytoplankton Summer Standing Crop and Annual Productivity as Functions of Phosphorus Loading and Various Physical Factors

RAY T. OGLESBY

Department of Natural Resources, New York State College of Agriculture and Life Sciences, Cornell University, Ithaca, N.Y. 14853, USA

OGLESBY, R. T. 1977. Phytoplankton summer standing crop and annual productivity as functions of phosphorus loading and various physical factors. J. Fish. Res. Board Can. 34: 2255–2270.

Relations of phytoplankton summer standing crop and annual productivity to morphometric properties and edaphic factors, especially phosphorus loading, have been examined for a large, diverse, globally distributed group of lakes. Standing crop was highly correlated with dissolved phosphorus loading when mixing of the water column was taken into account. A regression applicable to lakes of all depths is given as a log-log function with predictive confidence intervals for summer mean values. Boundary conditions for the exclusion of certain lakes have been roughly determined. For lakes of mean depth >25 m areal loading accounted for 97% of the variance in summer phytoplankton standing crop. Phosphorus inputs to shallower systems were adjusted to give a simple approximation of the influence of mixing processes and the ratio of bottom area to overlying water volume. Annual primary productivity seems to be a more complex and variable function of phosphorus loading than is summer standing crop. The former correlated fairly well with the morphoedaphic index. Productivity and standing crop showed well-defined trends in relation to other variables, but point scatter was so great that more exact definition of these functions was not justified.

Key words: phytoplankton, phosphorus, eutrophication, lakes, morphoedaphic index

OGLESBY, R. T. 1977. Phytoplankton summer standing crop and annual productivity as functions of phosphorus loading and various physical factors. J. Fish. Res. Board Can. 34: 2255–2270.

Nous avons examiné, dans un groupe important, diversifié et à distribution globale de lacs, les relations entre la biomasse estivale de phytoplancton et la productivité annuelle, d'une part, et les propriétés morphométriques et les facteurs édaphiques, en particulier la charge de phosphore, d'autre part. Il y a une haute corrélation entre la biomasse et la charge de phosphore quand on tient compte du mélange de la colonne d'eau. Nous présentons comme fonction log-log une régression applicable aux lacs à toutes les profondeurs, avec intervalles de confiance prévisionnels pour les valeurs moyennes d'été. Les conditions limites d'exclusion de certains lacs ont été grossièrement déterminées. Pour les lacs de profondeur moyenne >25 m, la charge est responsable de 97% de la variance dans la biomasse estivale de phytoplancton. Nous avons adapté les entrées de phosphore aux systèmes moins profonds, de façon à donner une approximation simple de l'influence des processus de mélange et du rapport de la superficie du fond au volume d'eau susjacent. La productivité primaire annuelle semble être une fonction plus complexe et plus variable de la charge de phosphore que ne l'est la biomasse estivale. Celle-là est en assez bonne corrélation avec l'indice morphoédaphique. La productivité et la biomasse montrent toutes deux des tendances bien définies par rapport aux autres variables, mais à cause de la grande dispersion des points, nous ne pouvons définir ces fonctions plus exactement.

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NUMEROUS attempts have been made by other researchers to define relations that would be useful in predicting the productivity of lake communities, especially their phytoplankton and fish components. Among factors potentially reflecting and/or determining productivity that have received attention are lake mean depth, content of dissolved solids, ratio of catchment area to lake volume (or its close analog, flushing time), incident light, and nutrient supply (especially phosphorus).

Recent studies on the response of phytoplankton standing crops in a group of New York lakes to phosphorus loading (Oglesby and Schaffner 1975) produced results encouraging enough to stimulate additional research into the generality of the rela-

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tionships defined and an extension to a consideration of primary productivity. My starting point in doing this is the working assumption that phosphorus supply is the principal determinant of phytoplankton standing crop and primary productivity in most lakes, a function modified by lake morphometry, light, and other influences.

In the following text specific relations describing the quantitative response of lake phytoplankton communities to phosphorus supplied from external sources and the modifying influences of lake environment have been developed using a simple stepwise approach. Initially, comparable data sets, derived from information in the extant literature and from personal communication with other researchers, were developed. Then, relations between certain factors other than phosphorus loading and phytoplankton growth and standing crop were examined independently, first for gross trends and next, where warranted, as mathematical functions. Finally, this information is used to develop a generality applicable within broadly specified boundary conditions.

Development of Data Sets

A variety of sampling and analytical methodologies have been and are being used to determine many of the variables examined. This meant that except for the New York lakes, data on some of the parameters were not precisely comparable. Decisions on which numbers to use and which to exclude were of necessity somewhat subjective. This introduced recognized but unquantifiable errors into the various relations examined below. To minimize bias induced by the several hypotheses, all decisions as to which data to accept were made prior to any attempt at establishing the relations between variables.

Several of the parameters used in the ensuing figures and equations were defined for the purpose of this research or have not been widely used in the literature. They are described, together with those that are more familiar, in Table 1. Items pertaining to phosphorus loading are discussed more fully below.

Data used in this study are given in Table 2 with references to information sources. Lakes are located as to country, in most cases a subdivision of the country, and latitude. If data represent an average for more than 1 yr, this is shown by the numbers in parentheses.

Phosphorus-loading information was sometimes given in the literature for a specific year or years in which case CHL_s pertains to the same period as that given for BAP input. In other instances loadings were calculated from information on drainage basin area, land use, population and the treatment afforded its sewage, industrial discharges, and atmospheric fallout according to a methodology developed for New York lakes (Oglesby and Schaffner 1975; Schaffner and Oglesby 1977) or general estimates applicable to a period of years were given by other researchers. For these situations CHL_s represents an average of all years within the approximate period for which data were available.

As explained below sets of data were omitted from inclusion in Table 2 if they were for lakes with summer color >30 Hazen units or for those with τ_ω <0.4 yr. An exception to the latter was Douglass Reservoir which was incorporated only in the comparison of CHL_s and annual productivity. Those lakes for which τ_ω is not given are assumed to have retention times >0.4 yr by virtue of their climatic regimes, ratio of catchment area to volume, and/or their similarity to other lakes for which retention time is known. If there is any instance where this assumption is incorrect, it is likely to be the Manitoba pothole lakes, whose hydrology is determined by groundwater flow.

TABLE 1. Description of parameters.

Symbol	Units	Definition and Use
CHL_s	$mg \cdot m^{-3}$	Mean chlorophyll *a* + phaeopigment concn in the upper 10 m of the water column, June–Aug. Taken as representative of the summer phytoplankton standing crop in northern latitude lakes.
1°	$g\ C \cdot m^{-2} \cdot yr^{-1}$	Annual primary productivity as determined by the ^{14}C uptake method.
$\bar{z}$	m	Mean depth of lake.
λ	$\mu S \cdot cm^{-1}$	Electrical conductivity. Usually given as specific conductance. When differences were noted between winter and summer, avg values for the latter were used.
MEI	$\mu S \cdot cm^{-1}$	Morphoedaphic index determined as the quotient of conductivity (used as an estimator of total dissolved solids) ÷ $\bar{z}$.
MEI_{z25}	$\mu S \cdot cm^{-1}$	Morphoedaphic index adjusted so that a max $\bar{z}$ of 25 m is assumed.
τ_ω	yr	Mean hydraulic retention time. Time required for an avg particle of water to transit a lake.
A_d	$m^2 \times 10^{-6}$	Area of drainage basin in millions of square meters (=km^2).
A_0	$m^2 \times 10^{-6}$	Area of lake in millions of square metres (=km^2).
V	$m^3 \times 10^{-6}$	Vol of lake in millions of cubic metres.
I_H	$J \cdot cm^{-2} \cdot day^{-1}$	Avg daily solar radiation incident on a lake's surface.
BAP	mg	"Biologically available" phosphorus, a composite of analytical species consisting of soluble reactive P + soluble unreactive P + that which desorbs into aqueous solution from suspended particulate material.
L'_{sp}[a]	$mg \cdot m^{-2} \cdot yr^{-1}$	Annual input of BAP per unit surface area of lake.
Λ'_{mp}[a]	$mg \cdot m^{-3} \cdot yr^{-1}$	Annual input of BAP calculated as being to a vol equivalent to that of the Aug. mixed zone, i.e. epilimnion of stratified lakes and total vol of those that are unstratified.

[a]Vollenweider (1968) used L_{sp} as the symbol for areal loading of total P. A superscript has been added to indicate BAP.

Morphoedaphic Factors

Mean Depth

Several extensive research projects were carried out by Canadian limnologists and fishery scientists during the 1950s in attempts to determine the influence of lake depth, among other factors, on faunal productivity, especially that of fish (Rawson 1952, 1955, 1960; Northcote and Larkin 1956; Hayes 1957). Close correlations were sometimes obtained

TABLE 2. Limnological data.

Lake Name	Location (and Reference)	CHL_a (mg m^{-3})	1° (gC $m^{-2}yr^{-1}$)	$\bar{z}$ (m)	ι (μScm^{-1})	MEI	τ_w (yr)	$\frac{A_o + A_s}{V}$	L_{1p} (mg $m^{-2}yr^{-1}$)	L_{mp} (mg $m^{-2}yr^{-1}$)
1. Conesus	U.S.A., 43°N (Oglesby et al. 1975, Oglesby and Schaffner 1975, Mills 1975)	6.3(3)	-	11.5	330	28.7	1.4	1.10	460	52
2. Hemlock	Same as (1) [Same as (33)]	6.4(3)	-	13.6	192	14.1	2.0	0.98	280	34
3. Canadice	Same as (1) (Oglesby et al. 1975, Oglesby and Schaffner 1975)	4.4	-	16.4	115	7.0	4.5	0.81	220	29
4. Honeoye	Same as (1) [Same as (33)]	15.2	-	4.9	166	33.9	0.6	2.90	300	61
5. Canandaigua	Same as (1) [Same as (33)]	2.6	-	38.8	295	7.3	7.4	0.27	280	29
6. Keuka	Same as (1) [Same as (33)]	3.3	-	30.5	226	7.4	6.3	0.31	320	32
7. Seneca	Same as (1) [Same as (33)]	7.7	-	88.6	769	8.7	18.1	0.09	490	43
8. Cayuga	Same as (1) (Oglesby et al. 1975, Oglesby and Schaffner 1975; Godfrey, Box 118, Laurens, N.Y., Pers. commun.)	8.8(2)	360	54.5	484	6.9	9.5	0.22	670	58
9. Owasco	Same as (1) [Same as (33)]	5.6(3)	-	29.3	262	8.8	3.1	0.64	660	59
10. Skaneateles	Same as (1) [Same as (33)]	7.4(3)	-	43.5	225	5.2	17.7	0.12	160	15
11. Otisco	Same as (1) [Same as (33)]	2.2	-	10.2	293	5.2	1.9	0.12	340	34
12. Oneida	Same as (1) (Wills et al. 1976, Greeson 1975)	25	-	6.8	302	40.4	0.6	2.50	650	95
13. Canadarago	Same as (1) (Nelling and Sykes 1971)	22.5	-	6.7	279	41.6	0.6	-	790	112
14. Otsego	Same as (1) [Same as (33)]	2.2	-	12.6	235	18.9	-	0.32	-	-
15. Waneta	U.S.A., 42°N [Same as (33)]	20.6	-	3.5	152	43.4	-	1.10	-	-
16. Lamoka	Same as (15) [Same as (33)]	7.3	-	5.0	150	30.0	-	1.43	-	-
17. Anderson-Cue	U.S.A., 39°N (Putnam et al. 1972)	4.3(3)	57.5	8	32	4.0	5.4	-	568(3)	71
18. McCloud	Same as (17) [Same as (17)]	3.4(3)	-	-	32	-	5.4	-	-	-
19. George	Uganda, 00°N (Viner and Smith 1973, Ganf and Viner 1973, Beadle 1974, Ganf 1974)	104	-	2.25	200	88.9	0.1	-	3215	540
20. Crose Mere	England, 53°N (Reynolds 1974a,b; Reynolds, FBA, Ambleside, Cumbria, England, Pers. commun.)	48.8(2)	-	4.8	346	72.1	2.0	3.24	1094	228
21. 885	Canada, 50°N [Same as (21)]	72(2)	-	1.5	1390	736	-	-	-	-
22. 154	(Sunde and Bertca 1975, Bertca 1975) Same as (21)	77(2)	-	2.3	1220	530	-	-	-	-
23. 302	[Same as (21)] Same as (21)	32.5(2)	-	2.9	1210	417	-	-	-	-
24. 255	[Same as (21)] Same as (21)	12.5(2)	-	1.7	852	501	-	-	-	-
25. 103	[Same as (21)] Same as (21)	60(2)	-	0.6	1043	1738	-	-	-	-
26. 979	[Same as (21)] Same as (21)	37	-	1.5	852	568	-	-	-	-
27. Okanagan	[Same as (21)] Canada, 50°N (Patalas and Salki 1973; Stockner and Northcote 1974)	5(2)	-	75.3	252	3.3	59	0.25	390	29.2
28. Osoyoos	Canada, 49°N [Same as (27)]	23(2)	-	20.7	250	17.9	0.7	6.24	2000	143
29. Kalmalka	Same as (27) [Same as (27)]	2.5(2)	-	58.0	369	5.3	71.3	0.02	320	32
30. Wood	Same as (27) (Patalas and Salki 1973, Stockner and Northcote 1974, Blanton 1973)	50(2)	-	21.0	295	13.8	-	1.25	-	-
31. Skaha	Same as (27) [Same as (27)]	31(2)	-	20.1	260	9.6	1.1	1.60	1400	140
32. Snagaea	U.S.A., 46°N (Malueg et al. 1975, Malueg, U.S. Environmental Protection Agency, Corvallis, Ore., Pers. commun.)	23.6(2)	-	5.7	55	14.9	1	2.23	338	121
33. Meretta	Canada, 75°N (Schindler et al. 1974a, Kalff and Welch 1974)	4.5(2)	11.3	1.25	160	49.2	-	-	81.5	11.3
34. Char	Same as (33) (Schindler et al. 1974b, Kalff and Welch 1974)	0.6	4.1	10.2	210	24.5	11.5	-	16	3.2
35. Washington	U.S.A., 48°N (Edmondson 1972, W. T. Edmondson, Univ. of Washington, Seattle, Wash., Pers. commun.)	22.5[a]	-	32.9	97	2.9	-	-	1760(3)	176
36. Leven	Scotland, 56°N (Smith 1974, Holden 1974, Bindloss 1974)	70(8)	780(4)	3.9	-	-	0.43	3.62	1104(4)	283
37. Neagh	Northern Ireland, 55°N (Stewart 1975, Gibson et al. 1971, Gibson, Dept. of Agriculture, Muckamore, Antrim, Pers. commun.)	39.6(4)	600	6.3	229	26.2	1.5	1.66	754	88.1
38. Bluehill South	Canada, 44°N (Kerekes 1972,1974)	1.2(2)	6.2	9.2	34	25.2	5.0	0.53	8	0.9
39. Yudle North	Canada, 48°N [Same as (38)]	1.2(2)	6.3	2.4	35	16.6	0.42	4.60	-	-
40. Esrom	Denmark, 56°N (Jónasson 1972; Jonasson et al. 1974)	-	140	12.3	310	25.2	9.0	0.48	605	50.4
41. Sammamish	Same as (35) (Welch et al. 1975a,b; Welch, Univ. of Washington, Seattle, Wash., Pers. commun.)	7.0(4)	230	17.7	-	-	2.2	0.76	221	29.5
42. Vombsjön	Sweden, 56°N (Gelin 1975)	47.9(2)	570(2)	5	350	58.3	0.8	5.10	-	-
43. Mountain	Canada, 46°N (Kerekes 1975a, Kerekes and Schwinghamer 1973, Kerekes, Environment Canada, Halifax, Nova Scotia, Pers. commun.)	1.1	-	4.3	23	5.2	0.8	-	-	-
44. Huron	U.S.-Canada, 44°N (Glooschenko et al. 1973, Berst and Spangler 1972, Ryder 1972)	2.5	65	60	160	2.6	-	0.77	-	-
45. Rabine	Canada, 55°N (Stockner and Shortreed 1975)	2	33	55.1	200	3.6	-	-	-	-
46. Vedro Leksjön	Sweden, 60°N (Holmgren 1968)	12	12	4.3	115	26.7	-	21.9	-	-
47. Vättern	Sweden, 58°N (Grimås et al. 1972, Ahl and Willén 1970)	2	122	37	96	2.5	-	0.09	-	-
48. Grafham Water	England, 52°N (Toms et al. 1975, Unpublished data)	3(5)		9.7	-	-	2.4	0.27	9215(5)	950
49. Norrviken	Sweden, 60°N (Holgren 1972, 1973)	65[a]	4(1)	5.4	-	-	0.8	6.76	2000	370
50. Cherokee	U.S.A., 36°N (Taylor 1971)	10.5	340	15.9	-	-	0.44	-	-	-
51. Douglass	Same as (50) [Same as (50)]	16.2	231	14.9	-	-	0.29	-	-	-
52. Norris	Same as (50) [Same as (50)]	3.3	88	22.9	-	-	0.76	-	-	-
53. Beech	Same as (50) [Same as (50)]	6.2	197	3.7	-	-	0.68	-	-	-
54. Nottely	Same as (50) [Same as (50)]	1.5	51	12.8	-	-	0.64	-	-	-
55. Magglore	Italy, 46°N (Monteo et al. 1970, Grimaldi 1972)		186(5)	177	135	0.6	6	0.18	-	-
56. Malaren	Sweden, 59°N [Same as (47)]	-	122	13	110	8.5	5	-	-	-
57. Mahinerangi	New Zealand, 46°S (Mitchell 1975)	-	52(2)	6.2	30	4.8	0.3	-	-	-
58. Ayyamgulan	India, 10°N (Sreenivasan 1964a, 1976)	-	3285	3	1222	407.3	-	-	-	-
59. Kodaikanal	Same as (58) [Sreenivasan 1964a,b]	-	164	2	27	13.5	-	-	-	-
60. Erie	U.S.-Canada, 42°N (Ryder 1972; Vollenweider et al. 1974)	-	245	18	242	13.4	-	-	-	-
61. Ontario	Same as (44) [Same as (60)]	-	185	60	272	3.4	-	-	-	-
62. Michigan	Same as (44) [Same as (60)]	-	145	84	226	2.7	-	-	-	-
63. Superior	U.S.A.-Canada, 47°N [Same as (60)]	-	90	146	75	0.5	-	-	-	-
64. ELA 114	Canada, 50°N (Brunskill and Schindler 1971, Schindler, Pers. commun.)	-	42	1.7	14	6.2	1.7	2.76	58	42
65. ELA 227	Same as (64) [Same as (64)]	-	108(4)	4.4	16	4.1	2.0	2.44	539(5)	122
66. ELA 239	Same as (64) [Same as (64)]	-	72(5)	10.5	22	2.3	5.4	0.53	64(4)	13
67. ELA 240	Same as (64) [Same as (66)]	-	47(5)	6.1	20	3.3	1.2	2.30	86(4)	16
68. ELA 261	Same as (68) [Same as (68)]	-	37(3)	2.9	15	5.2	1.2	2.66	193(4)	67
69. ELA 302N	Same as (64) [Same as (64)]	-	65	5.7	15	2.6	3.2	-	74	15
70. ELA 303	Same as (64) [Same as (64)]	-	30(2)	1.5	12	6.0	2.6	4.20	68(2)	45
71. ELA 304	Same as (64) [Same as (64)]	-	59	3.2	14	6.4	3.2	3.10	-	-
72. ELA 305	Same as (64) [Same as (66)]	-	96	15.1	22	1.4	30	0.30	-	-
73. ELA 302S	Same as (64) [Same as (64)]	-	58	5.1	15	2.9	3.2	-	82	16
Avg. ELA lakes except for Lake 227		-	54	5.8	17	2.8	6.6	-	96	33
74. Vorderer Finstertaler See	Austria, 47°N (Pechlaner 1966, Pechlaner et al. 1972)	-	66	14.8	25	1.7	0.5	-	-	-

[a]Data for 1957, 1962, and 1964.
[b]Data are for 1970.

for discrete groups of lakes but the general findings may be summarized with the quotation from Northcote and Larkin that "the only generalization which seemed justified was that quantities of fauna from lakes of great mean depth were never as high as those found in *some* lakes of low mean depth."

Sakamoto (1966) seems to have been the first to systematically examine the question of how summer phytoplankton standing crops are related to $\bar{z}$. For 10 Japanese lakes ranging in mean depth from 1 to 65 m, chlorophyll concentration in the euphotic zone decreased hyperbolically with increasing depth. Certain very shallow lakes containing dense macrophyte populations were exceptions. The information on Japanese lakes is not included in Table 2, since it represents only one or two samplings of each lake.

Mean depth was given a highly significant role by Vollenweider (1968) in his already classic paper relating trophic state to nutrient loading. In later versions the effects of depth are depicted as being modified by lake flushing rate (Vollenweider and Dillon 1974; Vollenweider 1975).

The principal reason for lake depth being considered as a significant influence on productivity rests with the assumption that nutrients are used more efficiently in shallow systems. If the bottoms of lakes are regarded as reservoirs as well as sinks for nutrients, then the shallower the water overlying the bottom sediments, the larger will be the amount of nutrients recycled from this source per unit volume of water in the lake. Such a process would be augmented by the wave induced stirring of sediments associated with low mean depth. Schindler (1975) has advanced an explanation for the rate at which lake eutrophication is reversed following decreased P supply based on the importance of recycled phosphorus from bottom sediments.

Sakamoto (1966) pointed out that in Japan shallower lakes tend to occur in fertile plains, while those of greater $\bar{z}$ are more often in barren mountain districts. Thus, a rough correlation with extraneous edaphic factors may be present in addition to the direct causal mechanisms relating mean depth to productivity.

Points in Fig. 1a represent a wide range of morphologies and trophic states for lakes located from the equator to north of the Arctic Circle. There is a general tendency for CHL_a to decrease with increasing depth, but the scatter of points is so great that any attempt at more detailed analysis does not seem worthwhile. A group of lakes characterized by low-incident solar radiation has very low standing crops coincident with low mean depth. Hereafter, those will be referred to as low-light lakes. The argument supporting this designation is developed below.

Primary productivity information is available for fewer lakes than is that for CHL_a, and in most instances one or the other, but not both, could be obtained for a particular body of water. For this reason 11 of the lakes shown in Fig. 1b are not included in the previous figure. A very general trend of decreasing 1° with increasing $\bar{z}$, at least for north temperate latitude lakes, exists up to a mean depth

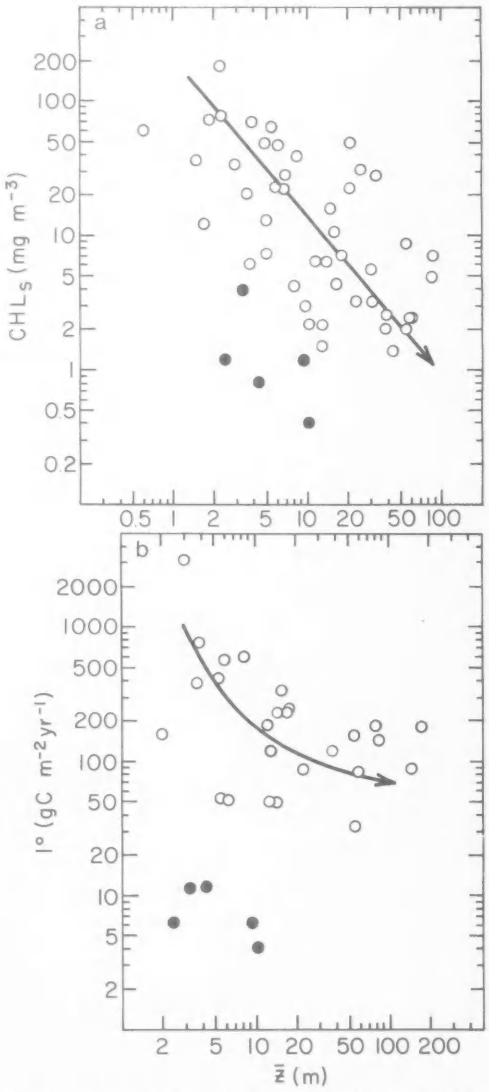


FIG. 1. a, Summer phytoplankton standing crop (CHL_s) as a function of mean depth ($\bar{z}$) for 51 lakes; b, annual primary productivity (1°) as a function of mean depth ($\bar{z}$) for 31 lakes. ●, low-light lakes; ○, all others. Trend lines are shown.

of about 25 m. Above this value productivity seems to be independent of depth. As with CHL_s, the primary productivity of those in the low-light category is lower than for other lakes of comparable depth.

CONDUCTIVITY

Several of the investigations referred to in the previous section included a test of the hypothesis that standing crops of various communities reflected the influence of edaphic factors as represented by the total dissolved solids (TDS) content of lakes. Rawson (1951, 1960) and Northcote and Larkin (1956) concluded that for lakes in central Canada and British Columbia, respectively, the production of net plankton, benthic organisms, and fish increased with increasing TDS. Their data exhibited considerable scatter except for those few lakes with very low dissolved solids content. Hayes and Anthony (1964) developed an index of fish productivity from multiple regressions that included alkalinity (roughly proportional to TDS or conductivity) as one of the independent variables. The single regression of their productivity index against alkalinity was not significant and accounted for only 18% of the total variance in the multiple regression. They cite other work by Ball (1945), who found no significant correlation between alkalinity and the abundance of fish in 32 Michigan lakes.

In the past, total dissolved solids, total alkalinity, and conductivity have been examined as potential correlates of lake productivity because they were readily measured indices of the edaphic factors influencing lakes. It was presumed that total dissolved solids, or some index of this, varied in direct proportion to essential nutrients such as phosphorus and nitrogen.

While it does seem logical that a very general proportionality of this type exists, numerous exceptions are known or can be readily postulated. For example, Dillon and Kirchner (1975) present evidence that drainage from plutonic rock formations is higher in phosphorus than that from sedimentary rocks, yet the total dissolved solids content of water draining the latter would generally be higher. Other cases are known where water entering a lake passes over and through highly soluble strata that contain virtually no primary plant nutrients, so that ionic content is not reflective of the fertilizing potential. Seneca and Cayuaga lakes in New York State are examples of this with NaCl concentrations reflecting inputs of wastes from salt mining and possibly subsurface inflows of saline water (Oglesby et al. 1975). At the other extreme, inputs of municipal sewage have extremely high nutrient levels in proportion to total dissolved solids and this may be true to an even greater extent for effluents from certain industries, e.g. see Hoden (1974) for the case of a woolen mill discharge to Loch Leven.

As in the case of $\bar{z}$, CHL_s generally tends to increase with increasing conductivity (Fig. 2a). At λ below 100–200 $\mu S \cdot cm^{-1}$ primary productivity does not seem to change as a function of ion content. Above this range there is a tendency towards higher 1° with increasing λ. As with $\bar{z}$, the low-light bodies of water exhibit lower standing crops and rates of production that place them in a category distinct from that for most other lakes. Both measures of

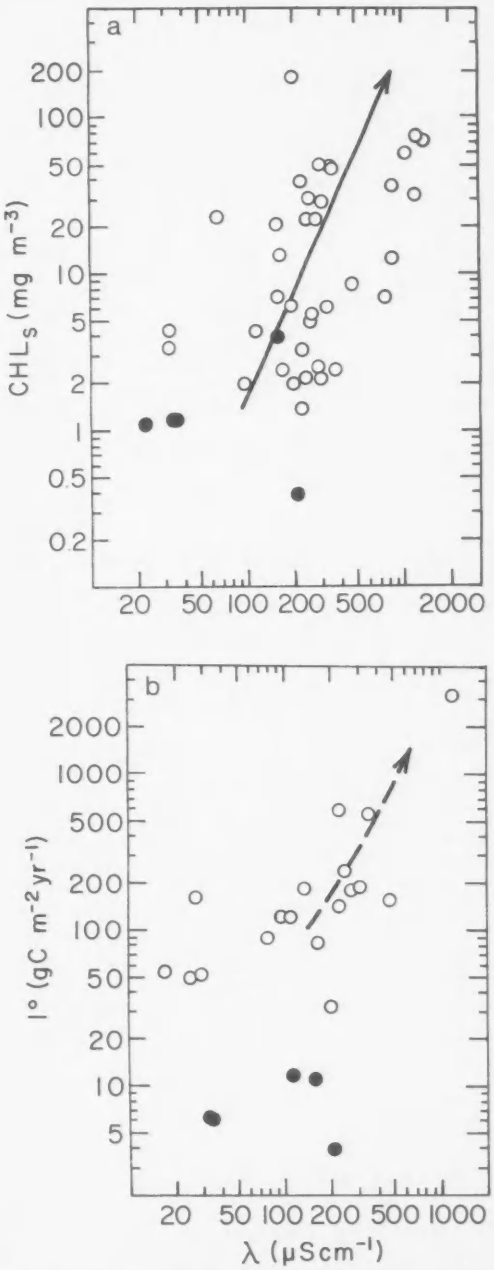


FIG. 2. a, Summer phytoplankton standing crop (CHL_s) as a function of conductivity for 42 lakes; b, annual primary productivity (1°) as a function of conductivity (λ) for 24 lakes. ●, those receiving low-light; ○, all others. Trend lines are shown with that for 1° being tentative and excluding low-light lakes and those with $\lambda < 150\ \mu S \cdot cm^{-1}$.

phytoplankton appear to be independent of λ for this group.

MORPHOEDAPHIC INDEX

The trends of increasing productivity with increasing TDS (or λ) and decreasing productivity with increasing depth were combined as a single proportion by Ryder (1961). He termed this ratio ($TDS/\bar{z}$ or $\lambda/\bar{z}$) the morphoedaphic index (MEI). Subsequent use of the MEI as a predictor of fish production has been reviewed by Ryder et al. (1974) and briefly criticized by Oglesby (1976). Insofar as could be determined no previous attempts have been made to examine correlates of MEI with phytoplankton productivity.

A potential association between $\bar{z}$ and edaphic influences has already been alluded to. When this is examined for the lakes in Table 2 through a determination of the correlation between $\bar{z}$ (dependent variable) and λ (independent variable), only a weak relation between the two emerges ($r = 0.27$, $\lambda = 53$ at $\alpha = 0.05$). If a relatively strong degree of independence between depth and edaphic factors is assumed from this evidence, the MEI provides a way of coupling these two factors which previous evidence shows may be broadly linked with CHL_s and 1°. Both $\bar{z}$ and λ range over about two orders of magnitude (Table 2), so that the use of a simple ratio of the two gives them each about equal weighting, an arbitrary and probably not the optimal decision if the slopes and curvatures of the trend lines in Fig. 1 and 2 can be relied on.

In assessing the relation of summer standing crop to MEI it was noted that the depth factor pulled the points representing very deep lakes away from the trend line. Presuming that depth became irrelevant past a certain point, an upper limit of 25 m was placed on $\bar{z}$; that is, those lakes with a mean depth greater than 25 m were assigned a $\bar{z}$ value of 25 m for purposes of computing a modified morphoedaphic index, designated as $MEI_{\bar{z}25}$. A plot of CHL_s against $MEI_{\bar{z}25}$ (Fig. 3a) shows that lakes in the low-light category are somewhat separated from the rest, and another group, consisting of the Manitoba pothole lakes, also deviates from the trend line suggested for the others. The Manitoba lakes conformed to the general trends for CHL_s as a function of both $\bar{z}$ and λ considered singly. Their displacement as a group in Fig. 3a seems to indicate the unsuitability of the MEI in characterizing lakes of this type, i.e. extreme shallowness combined with very high conductivity.

Scatter was low enough to warrant calculation of a regression in the plot of 1° as a function of $MEI_{\bar{z}25}$ (Fig. 3b). With low-light lakes excluded this was

(1) $\log 1° = 1.60 + 0.56 \log MEI_{\bar{z}25}$; $n = 19$; $r^2 = 0.59$

CATCHMENT AREA/LAKE VOLUME

A final relation between purely morphological and

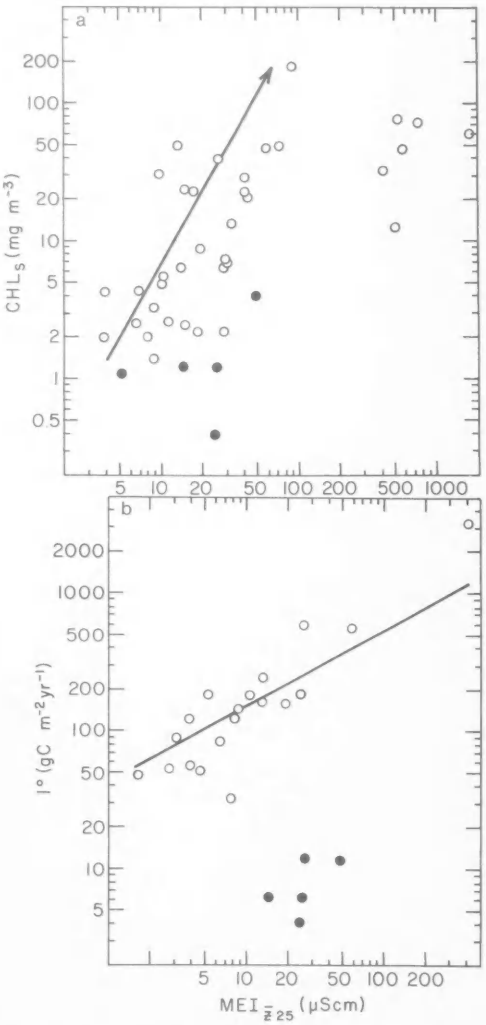


FIG. 3. a, Summer phytoplankton standing crop (CHL_s) as a function of the morphoedaphic index adjusted to a maximum $\bar{z}$ of 25 m ($MEI_{\bar{z}25}$) for 41 lakes; b, annual primary productivity (1°) as a function of the adjusted morphoedaphic index ($MEI_{\bar{z}25}$) for 24 lakes. A trend line is shown in (a) for all lakes except those in the low-light category (●) and the Manitoba potholes (grouped to the right side of the figure). The regression in (b) excludes low-light lakes.

edaphic factors and lake productivity to be reviewed is that hypothesized by Schindler (1971). He suggested that phosphorus inputs to lakes from runoff and atmospheric fallout were a function of the area of the catchment as modified by lake volume $[(A_d + A_0)/V]$.

Schindler (1971) tested his postulates by determining regressions expressing the dependence of various estimators and indices of productivity for the Experimental Lakes Area (ELA) lakes, northwestern Ontario. While a number of statistically significant regressions were obtained, data scatter was considerable. Schindler noted that relations of productivity to $(A_d + A_0)/V$ "would be expected to apply only for an area such as the ELA where the 'yield' of organic material or nutrient per unit area of terrestrial drainage is likely to be similar for all basins."

Defining "similar" basins is a subjective process. However, $(A_d + A_0)/V$ is not a very good predictor of CHL_s for two sets of similar lakes, those located in the Okanagan Valley of British Columbia and the Finger Lakes of New York (Fig. 4a). The other point to be noted for this figure is the broad curvilinear trend towards higher CHL_s at larger $(A_d + A_0)/V$ but with little or no change occurring until values for the latter exceed about 0.5–1.0.

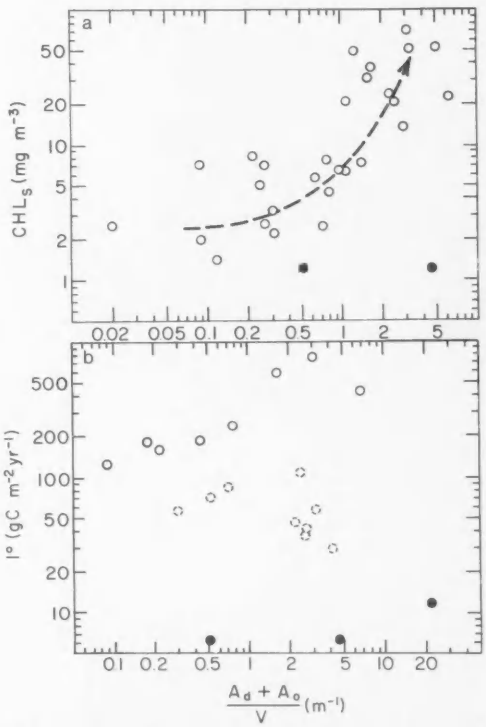
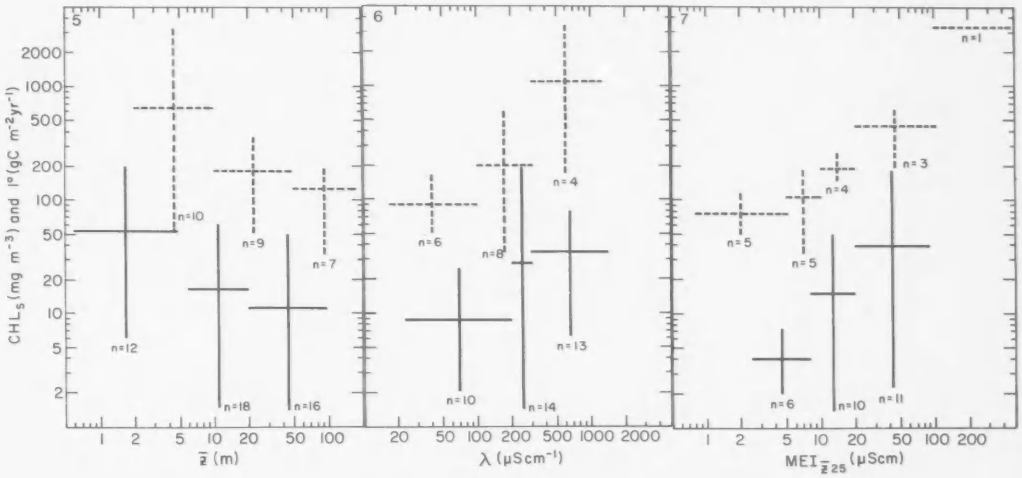


FIG. 4. a, Standing crops of phytoplankton during the summer (CHL_s) as a function of catchment area to lake volume ratio $[(A_d + A_0)/V]$; b, annual primary productivity (1°) as a function of catchment area to lake volume ratio $[(A_d + A_0)/V]$. A rough trend line is shown in (a). Low-light (●), ELA (◌), all other lakes (○).



FIGURES 5–7.

Frequency distribution of summer phytoplankton standing crops (CHL_s, solid lines) and annual primary productivity (1°, dotted lines) in relation to lake mean depth ($\bar{z}$) in Fig. 5, conductivity (λ) in Fig. 6, and the morphoedaphic index (MEI) in Fig. 7. Intersections of lines occur at class means. Number of observations in each class is indicated below the vertical lines depicting CHL_s and 1° ranges.

Primary productivity (Fig. 4b) shows no overall pattern as a function of catchment area to lake volume ratio. A tendency towards a positive correlation can be seen when the low-light and ELA lakes are excluded from consideration. The ELA lakes show, if anything, a negative response in productivity to increasing $(A_d + A_0)/V$. The upper point in this group (ELA 227 with 1° of 108 g C·m^{-2}·yr^{-1}) represents the only one of these lakes for which nutrient input has been artificially increased.

Overview of Morphoedaphic Factors

Continuing speculation in the literature concerning the influence of depth and dissolved solids content on lake productivity and the difficulty others have had in trying to define such questions impart significance to the general trends and the degree of deviation from these shown in Fig. 1–3. Except in the case of 1° as a function of MEI the only further reduction of data that seems worthwhile at this time is that presented in Fig. 5–7. This consists of frequency distributions on a log-log scale with class intervals chosen to balance the desirability of having constant numbers of observations in each against that of using constant class size.

The following generalizations emerge from a consideration of Fig. 5–7: (1) As the mean depth of lakes increase summer phytoplankton standing crop and primary productivity are likely to be lower and the reverse is true with increasing conductivity (equated with TDS) and morphoedaphic index values. The ranges of both phytoplankton parameters overlap so greatly between class intervals that no assumptions about where an individual lake would be predicted to fit are justified. The means of broad class intervals appear to be significantly different, but this assumption could not be tested because of differing variances about the means. (2) Trends of change in CHL_s appear to be approximately linear functions of $\bar{z}$, λ, and MEI on a log-log scale, i.e. hyperbolic on an arithmetic scale. Those for 1° are slightly curvilinear. Broadly similar slopes for 1° and standing crop indicate roughly parallel changes in the two parameters. (3) The large scatter of points about trend lines suggests that neither mean depth nor dissolved solids are primary determinants of phytoplankton concentration and growth but rather play a secondary role as modifiers of lake response to nutrient supply.

Other Physical Factors

Hydraulic Retention Time

The water retention time (τ_ω) of a lake potentially affects its productivity through influences on the input and output of nutrients and by the washout of phytoplankton. The inflow of water and nutrients is inherently coupled to $(A_d + A_0)/V$, the theoretical renewal time being usually calculated as the ratio of the total catchment times the difference between precipitation and evapotranspirative losses divided by lake volume (Brunskill and Schindler 1971). In the previous section it was shown that the assump-

tion of nutrient supply changing as a function of $(A_d + A_0)/V$ was a poorly defined relation if phytoplankton standing crop and production are assumed to reflect nutrient loading.

The other factor involved with τ_ω, the washout of phytoplankton, becomes increasingly important as the rate at which cells are flushed from the system approaches the growth rate, probably on the order of days or weeks for a natural community. Mathematical treatments of the problem have been developed only for idealized, completely mixed or piston flow systems containing pure cultures of microorganisms (Herbert 1969), so an empirical solution offers the only practical route to estimating the quantitative effects of τ_ω on phytoplankton in lakes.

The actual point at which τ_ω becomes a significant factor to phytoplankton standing crops and production through either or both of these mechanisms is not well defined by the literature, but some clues can be found. Dickman (1969) provided some of the first evidence that τ_ω could be of significance in certain cases with his studies of a small British Columbia lake which was flushed as quickly as once every 2.5 days during periods of high precipitation. Dillon (1975) demonstrated that phytoplankton standing crop in a rapidly flushed Ontario lake (τ_ω <0.1 yr) was much below that anticipated from phosphorus loading data. He proposed an expression incorporating a phosphorus retention coefficient and flushing rate to correct loading estimates for the effects of lake hydrology. Kerekes (1973; 1975b) obtained indications from studies of Newfoundland and Nova Scotia lakes that at water retention times <0.2–0.4 yr chlorophyll concentration and total phosphorus, a correlate of phytoplankton standing crop, became a function of flushing rate.

Vollenweider (1975) has provided a theoretical basis for the influence of hydraulic retention time on lake productivity. Later versions of his phosphorus loading–$\bar{z}$–trophic state relation are modified to include τ_ω as a factor acting together with depth to influence lake response (Vollenweider and Dillon 1974; Vollenweider 1976).

Since in most cases volume is proportional to $\bar{z}$ and τ_ω is a function of lake volume, the expansion of the depth term to incorporate this hydraulic parameter approximates the insertion of a constant, important exceptions being lakes with unusually high $(A_d + A_0)/V$ and those located in climates with a large surplus of precipitation over evapotranspiration. In North America, lakes in the latter category are largely confined to a narrow strip along the Pacific northwest coast of the United States and British Columbia, Canada, and in the maritime provinces of eastern Canada.

Kerekes (1973) suggests one other possible set of circumstances where τ_ω might have important implications for lake productivity. This is the case of shallow lakes in arid climates, where relatively long retention times may result in the establishment of highly saline conditions potentially inhibitory to phytoplankton growth. In view of situations reported for some of the lakes in Africa with very high salinities coinciding with phytoplankton concentrations among the highest reported in the world (Beadle 1974) it would seem that any such inhibitory effect would result from unusual combinations of ions rather than their total quantity.

If the concept that τ_ω becomes important to standing crop of phytoplankton only at high rates of nutrient dilution and/or phytoplankton washout is accepted as a working hypothesis, where is the point at which τ_ω becomes critical? No precise answer to this question is possible due to complications engendered by factors such as lake trophic state, short-circuiting of flow, and the timing of inflow over the course of a year. Since our present understanding is insufficient for these details to be considered, the expedient was adapted of excluding from consideration all lakes with τ_ω <0.4 yr, a value thought to be conservative in view of existing information on short retention time lakes. Of the longer retention time lakes for which data were available τ_ω varied between 0.42 and 71.3 yr (Table 2). An examination of the various relations depicted in Fig. 1–4 does not reveal any bias due to differences in mean hydraulic retention time within this range of values.

Light

The light available for photosynthesis in a lake over the course of a year is a function of (1) incident solar radiation (I_H), itself dependent on latitude and climatic conditions; (2) transparency, thickness, and duration of ice and snow cover, if any; (3) reflection from the water surface which varies in relation to ripple and wave action and solar angle; (4) optical properties of the water including light absorption by agents such as humic-like colloids and absorption and reflection by suspended particulate material; and (5) absorption by the bottom of any radiation that penetrates that far. Only by frequent measurement of light profiles can the light available for photosynthesis be determined with any precision and such data are relatively rare for the lakes considered in this study. However, a rough approximation of the light regime could be made from information on I_H and several other factors.

Six of the lakes (Meretta, Char, Nedre Laksjön, Bluehill South, Yudle North, and Mountain) are separately symbolized in the figures and are categorized as being those with low-light regimes. The data in Table 3 represent the only reliable ones that could be obtained on incident light but are sufficient to provide evidence supporting the foregoing designation.

The low-incident radiation characterizing Char

TABLE 3. Average daily solar radiation (I_H) received by some of the lakes listed in Table 2. Lakes are listed in order of increasing latitude. Vorderer Finstertaler is the only one located at a high altitude (2237 m).

Lake	Lat.	I_H ($J \cdot cm^{-2} \cdot day^{-1}$)
George	00°00′	1970
Cayuga	42°41′	1561
Sammamish	46°36′	1460
Vorderer Finstertaler	47°12′	1703
Shagawa	47°55′	1217
Bluehill South and Yudle North	48°30′	468[a]
Manitoba pothole lakes	50°30′	1533
Esrom	56°	1147
Vombsjön	56°	1033
Char and Meretta	74°42′	552

[a]In the photosynthetic range. This is about 50% of total I_H (Strickland 1958).

and Meretta lakes is a function of their extreme northern latitude, while that of Bluehill South and Yudle North is determined more by climate. Kerekes (1972) states that at Gander, Newfoundland, cloud cover averaged 79%. Although there are no radiation data for lakes Nedre Laksjön (68° N) and Mountain (44° N), these would be expected to fall, respectively, into the two categories of low-light lakes cited above. In addition to latitudinal and climatic effects, the light actually available to organisms in the lakes cited would be further limited for those in the arctic by prolonged ice and snow cover (ranging from 300 to 365 days for Char and Meretta, 1969–72) and by water being moderately colored (10–20 Hazen units during the summer and higher in winter) in Yudle North, Bluehill South, and Mountain lakes.

Both the quality (e.g. size) and concentration of suspended material affect the light regime of lakes, and descriptions are available of some instances where their influence on phytoplankton has been significant. Cheng and Tyler (1976) found that high turbidity exerted a controlling effect on primary productivity in Lake Crescent, Tasmania. In comparing this with Lake Sorell the former has 10 times as high a standing crop but only 2.6 times as high a productivity, a difference they attribute to attenuation of light by suspended matter in Lake Crescent. Marzolf and Osborne (1972) concluded that 1° in Tuttle Creek Reservoir, located on the Great Plains of the United States, was probably limited by light exclusion due to turbidity. Gulati (1972) described the case of a lake in the Netherlands, Wijde Blik, where sand and silt stirred up from the bottom by wind and by sand dredging caused persistent high turbidity. Primary productivity was on the order of 100 g $C \cdot m^{-2} \cdot yr^{-1}$, much lower than would be anticipated from the winter total phosphorus concentration of 50 $mg \cdot m^{-3}$.

Where information was given it was apparent that none of the lakes listed in Table 2 were subject to persistent high turbidities during the algal growing season. An absence of data or remarks concerning suspended material was taken as evidence that the remainder should not be categorized as turbid. Self-shading is another way in which phytoplankton populations can be limited by the light-absorbing actions of suspended material. Of those in Table 2 only Lake George seems to approach this point (Ganf 1974).

Phosphorus Loading and Summer Phytoplankton Standing Crop

The original premise of this research is that CHL_s and 1° are primarily controlled by the supply of phosphorus from external sources. Before describing the results bearing on this postulate the reader is reminded that phosphorus loadings are calculated in terms of the sum of soluble and potentially soluble species (BAP), not as total phosphorus, which most other researchers have used. Oglesby and Schaffner (1975) and Bouldin et al. (1975) have argued that total phosphorus is inappropriate for this purpose, especially in situations where a substantial part of the input consists of P adsorbed to soil particles.

Using the method by which Oglesby and Schaffner (1975) estimated the BAP loadings for 13 New York lakes it has been possible to calculate annual P inputs, or in a few instances, inflows have been measured with sufficient frequency and in the proper form to provide L'_{sp} and Λ'_{mp} estimates for an additional 26 lakes. In a few cases, where loadings are dominated by sources of soluble P such as sewage treatment plant discharges or phosphorus carried in groundwater, published loadings given in terms of total P have been assumed to consist entirely of BAP. A few of the loading values published in the literature were rejected in toto because of evidence indicating probable large errors. For example, Patalas and Salki (1973) give a loading estimate for Lake Wood, one of those in the Okanagan chain, that was rejected because another investigator (Blanton 1973) has shown that large subsurface flow into this lake is likely. Personal experience has shown that groundwaters in the Columbia Plateau region may contain very high concentrations of dissolved phosphorus.

The relation of CHL_s to surface area loading of BAP is shown in Fig. 8. A trend towards higher chlorophyll concentrations with higher L'_{sp} is demonstrated, and the deep lakes adhere closely to the regression

$$(2) \quad \log CHL_s = -2.96 + 1.38 \log L'_{sp}; n = 10; r^2 = 0.97$$

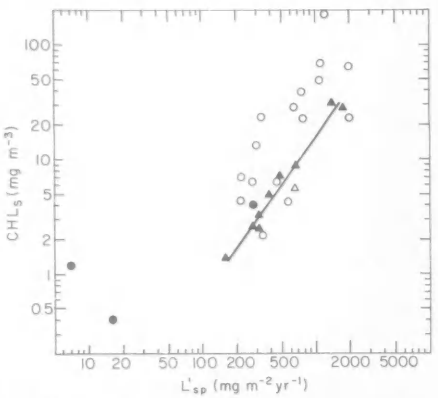


FIG. 8. Summer phytoplankton standing crop (CHL_s) as a function of "biologically available" phosphorus loading to lake surface area (L'_{sp}) for 29 lakes. ●, low-light lakes; ▲, those with $\bar{z} > 25$ m; ○, all others. The regression line for lakes of mean depth >25 m is shown.

Grafham Water, not shown (see Table 2), is the only one of the lakes for which this set of data was available, which deviates markedly from the general pattern. This is a pumped storage impoundment with most of its inflow coming from the Great Ouse, a river heavily polluted with sewage discharges. Unpublished data provided by the Water Research Centre, Stevenage (England), and the report of Toms et al. (1975) indicate a surfeit of all major nutrients and a number of essential trace elements. The following hypothesis is suggested to account for the very low algal standing crop observed relative to that which would be expected from nutrient supplies or even what is found in the Great Ouse (average CHL_s for 1969–73 equaled 34.8 mg·m^{-3}). Grafham Water is supersaturated with Ca^{++} (average concentration of 117 mg·ℓ^{-1}) to a considerably greater extent than any of the other lakes studied. This is probably made possible by the large amounts of CO_2 being produced by heterotrophic activity. The high concentrations of calcium and phosphorus combined with the fluctuating pH resulting from intense biological activity produce highly unstable conditions under which amorphous compounds such as octacalcium phosphate (Zoltek 1976) are formed. Such "chemically bound" phosphorus may still test as orthophosphate (the species determined in the Grafham Water study), thus accounting for the high concentrations observed in the impoundment, but it may not be available for biological uptake.

Returning to the general question of how P loading affects CHL_s a more linear relation than that in Fig. 8 was obtained when standing crop was examined as a function of $L'_{sp} \times MEI_{\bar{z}25}$. Excluding the low-light lakes the following regression was determined for the distribution shown in Fig. 9.

(3) $\log CHL_s = 0.16 + 0.85 \log (L'_{sp} \times MEI_{\bar{z}25})$;
$n = 22; r^2 = 0.68$

The effect of this modification of loading is to weight annual BAP supply positively for conductivity (≡total dissolved solids) and negatively for increasing depth up to a limit of 25 m.

The optimum function obtained for CHL_s was developed when loading was calculated as that of the summer mixed zone (Fig. 10). The shallower lakes ($\bar{z}$ from 2.25 to 17.7 m) are brought into line with these of $\bar{z} > 25$ m and the following regression, with lakes

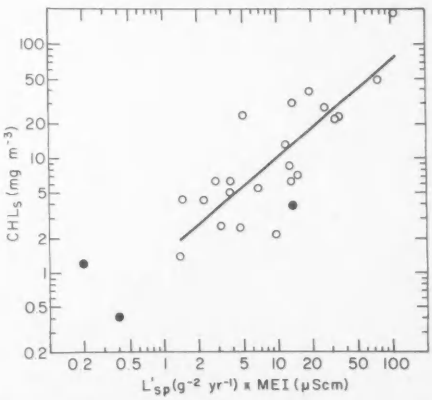


FIG. 9. Summer phytoplankton standing crop (CHL_s) as a function of the product of areal BAP loading (L'_{sp}) and the morphoedaphic index (MEI) for 25 lakes. The regression line for all lakes except those with low-light regimes (●) is shown.

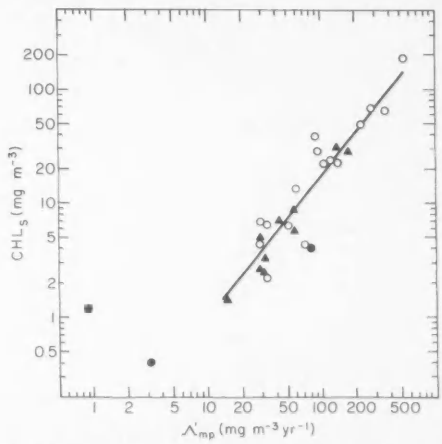


FIG. 10. The regression of summer phytoplankton standing crop (CHL_s) on the annual loading of BAP to the volume of the summer mixed zone (A'_{mp}) for 29 lakes. ●, low-light lakes; ▲, those with $\bar{z} > 25$ m; ○, all others. The former and Grafham Water (see Table 2) are excluded from the regression.

having a low-light regime and Grafham Water excluded, accounts for a greater percentage of the observed variance than does Equation 3:

$$(4)\quad \log CHL_s = -1.28 + 1.26 \log \Lambda'_{mp};\quad n = 25;\ r^2 = 0.96$$

The effect of calculating loading in this manner is to weight heavily for shallowness, especially in the case of unstratified lakes. The derivation of Λ'_{mp} and its rationale are discussed in more detail by Schaffner and Oglesby (1977) and Oglesby and Schaffner (1977).

Even when the low-light lakes are included, a highly significant relation between CHL_s and Λ'_{mp} ($\log CHL_s = -0.65 + 0.92 \log \Lambda'_{mp}$; $n = 28$; $r^2 = 0.82$) is apparent. Surprisingly, tropical Lake George, Uganda, fits the regression well despite the fact that "summer" has little meaning for this lake, its chlorophyll content being essentially constant at about 190 mg·m^{-3} throughout the year.

Of the lakes depicted in Fig. 8–10 data on annual primary productivity were available for only nine, and three of these are categorized as receiving low-incident solar radiation. Adding an additional group, those of the Experimental Lakes Area, produces the ill-defined relation between 1° and Λ'_{mp} shown in Fig. 11.

Another approach to defining the dependence of 1° on Λ'_{mp} is to seek a relation between the former and CHL_s (Fig. 12) which could then be used to convert standing crop to productivity data. Brylinsky and Mann (1973) present a graph of log productivity as a function of log chlorophyll *a* concentration, both values being for the growing season, which strongly suggests an interdependence of the two variables but with points exhibiting considerable scatter. A reasonably good approximation of CHL_s as a function of 1° is provided by the equation $y = 0.0019\ x^{1.61}$ (Fig. 12, solid line). However, the broken line more closely fits the points and its shape is of interest, since decreased photosynthetic efficiency (production per unit chlorophyll) is suggested at higher standing crop values. This is a logical development, one that also seems to be reflected in the distribution of data given by Brylinsky and Mann and is a phenomenon that Talling (1975) cites as having been reported by some other researchers. The four points representing low-light lakes are also interesting. Comparing the slope of their trend line with that for other lakes suggests that phytoplankton communities in the former have a lower photosynthetic efficiency. In view of the apparent complexity in the CHL_s – 1° relation, interconversion of these two parameters seems premature at this time.

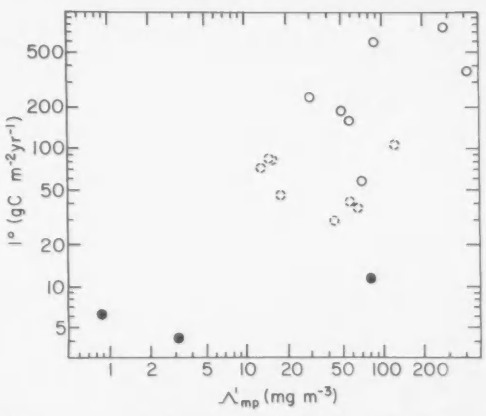


FIG. 11. Annual primary productivity (1°) as a function of loading of BAP to the volume of the summer mixed zone (Λ'_{mp}) for 18 lakes. ◌, ELA lakes; ●, those in the low-light category; ○, all others.

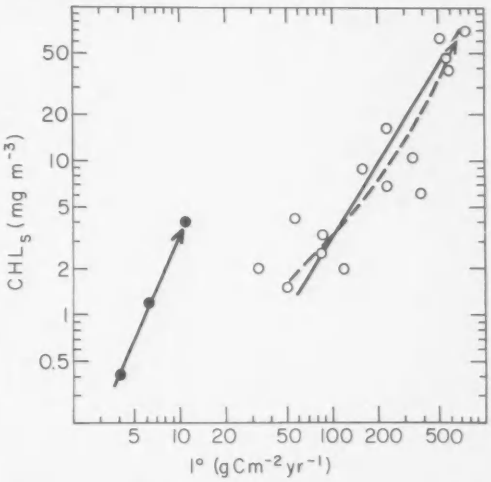


FIG. 12. Relation of summer phytoplankton standing crop (CHL_s) and annual primary productivity (1°) for 19 lakes. A trend line for low-light (●) lakes and one for others (broken curve fitting open circles) are shown together with a linear approximation for the latter (solid line).

Discussion

Equation 4 (Fig. 13) provides a simple expression of how mean summer phytoplankton standing crop varies between lakes solely as a function of the BAP supplied from external sources as modified by the effects of depth. It does so with surprising precision considering that lakes ranging over such a wide spectrum of morphologies, trophic states, hydrologies, and light regimes are represented. Success in developing such a well-defined relation was due to the use of BAP (rather than total P) in calculating inputs, the development of a loading expression that accurately reflected the effect of depth, the estab-

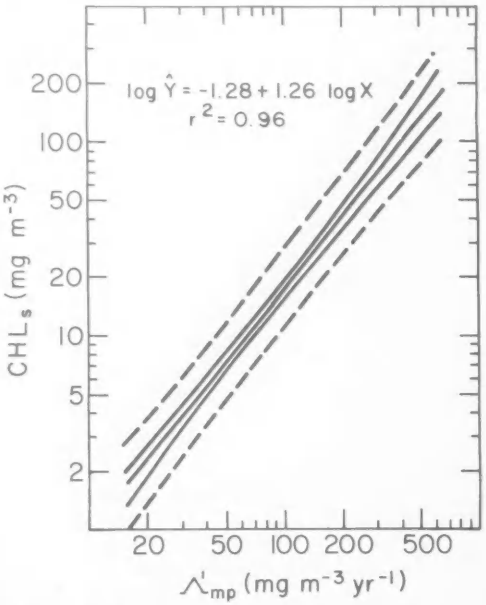


FIG. 13. Regression of summer phytoplankton standing crop (CHL_s) on annual mixed zone loading of BAP (Λ'_{mp}) showing 95% confidence intervals (——) and predictive confidence intervals (----).

lishment of rough boundary conditions that excluded certain categories of lakes, and the fact that data sets for some other types of lakes were not available.

The first two of the above factors were largely determined by the research on New York lakes (Oglesby and Schaffner 1975, 1977; Schaffner and Oglesby 1977). The weighting of loading for depth relates functionally to mixing processes as well as to the ratio of sediment area to overlying lake volume. The simple example given in Table 4 illustrates how the effect of shallowness increases exponentially as mixing depth decreases arithmetically.

Criteria for determining which lakes would likely be unsuitable for inclusion in Equation 4 were arrived at in two ways. Graphs involving morphoedaphic factors were scrutinized for individual lakes or groups of lakes deviating from the general trend. Those found were placed in an excluded category once a reasonable postulate concerning the reason for their uniqueness was arrived at. Also, factors that may be potentially limiting were evaluated from the available literature. Approximations of limits on minimum τ_ω and I_H were obtained in this way.

Among types of lakes not represented in Table 2 are those dominated by flora other than phytoplankton and those with persistent high turbidities. Of the lakes listed some, such as wide, shallow Oneida, have extensive macrophyte populations and at times are turbid, while others, e.g. deep, steep-sided Skaneateles, are almost free of higher plants and have little suspended inorganic materials except during rare circumstances. However, all should probably be characterized floristically as phytoplankton dominated and none are intrinsically turbid. The published literature is certainly adequate to indicate that dominance by other kinds of plants or high turbidities may limit CHL_s and 1° below expected levels, but quantitative boundaries cannot be established from the information available.

TABLE 4. Calculated loadings at constant P supply for idealized basins with vertical sides, surface areas of 1×10^{-6} m² and BAP inputs of 100 g·yr⁻¹ (L'_{sp} = 100 mg·m⁻²·yr⁻¹).

$\bar{z}$ (m)	Depth of Aug. mixed zone (m)	Λ'_{mp} (mg·m⁻³·yr⁻¹)
1	1	100
5	5	20
10	10	10
20	12	8.3
50	20	5
100	25	4

Other discrete factors potentially limiting phytoplankton standing crop and/or 1° that have so far not been considered are grazing and the role of nutrients other than phosphorus. In regards to zooplankton grazing, I have adopted the working premise that zooplankton are in balance with their food supply, assumed to be phytoplankton except in lakes grossly polluted with biodegradable organic matter or possibly for those that are very small and surrounded by dense vegetation. If this is so, the effects of grazing for an entire growing season or annually can be regarded as approximately constant and therefore ignored for purposes of generalized models such as that for CHL_s–Λ'_{mp}.

A detailed knowledge of seasonal changes in nutrient concentrations for some of the lakes listed in Table 2 would suggest that at times during the growing season available nitrogen and some of the trace elements might limit phytoplankton growth. Conesus and Hemlock lakes have undetectable concentrations of NO^-_3 N during much of the summer (Mills 1975; Oglesby et al. 1975) and a study of Cayuga revealed some of the lowest concentrations of trace elements reported for any lake in the world (Mills and Oglesby 1971). However, these and other

lakes with similar apparent deficiences of nutrients other than P still seem to have summer standing crops determined by phosphorus loading as evidenced by their fit to the regressions expressed by Equations 2–4.

The effect of lake depth on CHL_s seems to be constant at $\bar{z} > 25$ m. Thus, for deep lakes areal-loading data in terms of BAP are excellent predictors of summer phytoplankton standing crop, so that August mixing zone depth does not have to be defined. This is a considerable advantage, since clearly defining thermal structure is most difficult for large, deep lakes.

The complexity of the relation between CHL_s and 1° (Fig. 12) is probably one of the reasons that no well-defined function of the latter in terms of Λ'_{mp} could be obtained (Fig. 11). Nevertheless, BAP loading is obviously a more accurate predictor of standing crop than of annual productivity and this seems unlikely to change with the addition of more data. The information developed so far also suggests that the $1°$–Λ'_{mp} function is probably curvilinear even on a log-log plot with a decreased rate of change of 1° in response to phosphorus loading at higher levels.

The linear change of CHL_s in comparison with the slight curvilinearity of 1° functions, seen in most of the morphoedaphic graphs as well as in the relation of CHL_s to primary productivity, must reflect a fundamental difference between the responses of these two parameters to a variety of environmental factors. Differences seem to be most pronounced for lakes that are shallow, have high dissolved solids contents, have a high catchment area to lake volume ratio, or have higher than average BAP loadings.

Vollenweider (1976), using data for 60 lakes, has developed a log-log regression for average epilimnetic chlorophyll concentration as a function of total phosphorus loading expressed so as to take into account the influences of basin and lake hydrology. While his relationship is not directly comparable with those shown in Fig. 10 and 13, the two approaches would appear to provide about equal predictability of phytoplankton standing crops for lakes in the mesotrophic range but the latters give better estimates for those that are eutrophic. Vollenweider includes a number of highly oligotrophic systems (epilimnetic chlorophyll <1 mg·m^{-3}) for which there is no analog in Figures 10 and 13.

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Relationships of Fish Yield to Lake Phytoplankton Standing Crop, Production, and Morphoedaphic Factors

RAY T. OGLESBY

Department of Natural Resources, New York State College of Agriculture and Life Sciences, Cornell University, Ithaca, N.Y. 14853, USA

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Fish yield is related to annual primary production, summer phytoplankton standing crop, and the morphoedaphic index for lakes representing a wide variety of typologies by a series of models in the form of log-log regressions. Tentative boundary conditions are established by which lakes inappropriate to the models can be excluded. Confidence intervals for predicted values about the mean are given for the fish yield–phytoplankton standing crop regression. From this relation, potential yields for the lakes studied are reduced from a range of 10,000 to one of 25-fold. Efficiencies with which carbon is transferred from primary production to fish yield vary by 2 to 3 orders of magnitude and are highest for small, intensively managed ponds and lowest for large, deep, cold-water lakes. Models based upon fish yield as a function of phytoplankton production or standing crop are inherently more accurate and subject to fewer exceptions than are those related to morphoedaphic factors. The former appear to be capable of substantial refinement but even in their present state might be employed to make useful predictions for groups of lakes. A suggested supplement to existing approaches in fishery management involves the following sequence: (1) use of expectation-variability diagrams to obtain an overview of the problem, (2) selection of an appropriate model or models to predict yield, (3) prediction of a range of yields, and (4) implementation of regulations proved successful for other lakes in the same yield category.

Key words: fish, lakes, phytoplankton, morphoedaphic index, fishery management

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A l'aide d'une série de modèles ayant la forme de régressions log-log, nous établissons la relation entre le rendement en poisson et la production primaire, la biomasse estivale de phytoplancton et l'indice morphoédaphique dans des lacs représentant une gamme variée de typologies. Nous établissons les conditions limites provisoires permettant d'exclure les lacs inappropriés aux modèles. Nous indiquons les intervalles de confiance des valeurs prédites autour de la moyenne pour la régression rendement en poisson–biomasse de phytoplancton. A partir de cette relation, les rendements potentiels des lacs étudiés sont réduits d'une gamme de 10 000 à une gamme de 25 fois. L'efficacité avec laquelle le carbone passe de la production primaire au rendement en poisson varie de 2 à 3 ordres de grandeur, et est maximale dans les petits étangs soumis à une gestion intensive et minimale dans les grands lacs d'eau froide profonds. Les modèles fondés sur le rendement en poisson comme fonction de la production ou de la biomasse de phytoplancton ont une précision inhérente plus grande et sont sujets à moins d'exceptions que les modèles fondés sur les facteurs morphoédaphiques. Les premiers semblent susceptibles d'un raffinement substantiel mais, même dans leur état présent, peuvent être utilisés pour des prédictions applicables à des groupes de lacs. Un complément que nous suggérons aux approches existantes à la gestion des pêches comprend les étapes suivantes : (1) l'utilisation de diagrammes anticipation-variabilité afin d'obtenir une vue d'ensemble du problème, (2) le choix d'un modèle ou de modèles appropriés afin de prédire le rendement, (3) les prédictions d'une gamme de rendements et (4) l'application de règlements qui ont réussi dans d'autres lacs de même catégorie de rendement.

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BOTH fisheries and limnological literature contain many references to the possible effects of increased phytoplankton productivity on the fish communities of lakes. Most of the statements are based on deductions concerning systems in disequilibria from a number of stresses and tend to be presented as generalities unaccompanied by substantive data. As

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valuable fisheries have collapsed in lakes subject to high levels of human influence, attention in North America and Scandinavia and European countries has focused on the detrimental effects of eutrophication (e.g. Loftus and Regier 1972). In other parts of the world particular stress is being placed on ways in which the total yield of fish protein can be increased, and management techniques include deliberate fertilization to increase productivity (e.g. Hepher 1962; Pillay 1966).

The intention of this article is to consider fish yield, the only measure of fish production for which there is information from a large number of different lakes, as a function of phytoplankton production and standing crop. Other workers (Ryder 1965; Ryder et al. 1974; Welcomme 1976) have related fish yield to morphoedaphic factors. The most commonly used measure of these is compared with summer phytoplankton concentration and annual productivity as possible predictors of fish yield.

Description of Data Used and Sources of Error

Most of the symbols are those used by Oglesby (1977, this issue). New symbols are Y (general notation for annual yield of fish per unit area), Y_f (annual yield of fish, expressed as dry weight per square metre of lake surface), and Y_{fc} (annual yield of fish, as carbon per square metre).

Yield has been used by many workers as an index of fish production. Ryder et al. (1974) state that a criterion for yield to be used in models such as theirs (Y as a function of MEI) is that lakes must be subject to moderately intensive to intensive fishing pressure, a property often difficult to establish from the literature. Unfortunately, if a large number of lakes are to be compared there are no alternatives to yield as a fishery estimator, since production and biomass estimates are rare and, even when available, their accuracy is often highly questionable.

I have expressed yield as dry weight (Y_f) for its appropriateness to other research on the relation of Y_f to production and standing crops of zooplankton and benthos or as Y_{fc} so that efficiencies with which photosynthetically fixed carbon is transformed to fish yield could be estimated. Yield (Y_f) was calculated as being 75% wet wt and Y_{fc} is based on the assumption that 1 g C equals 10 g wet wt (or 2.5 g dry wt) of fish (Rodhe 1958).

Summer standing crop (CHL_s) and annual production (1°) were chosen as phytoplankton community descriptors because of data availability and other reasons. Of the two, CHL_s estimates are probably more reliable than are those of 1° because of more accurate analytical methodologies and greater spatial and temporal coverage. Summer chlorophyll is intended as a rough index of annual production on the one hand and as an indirect estimator of the food available for fish on the other. This rationale for CHL_s takes on a different meaning for lakes in the tropics, since "summer" for such bodies of water is characterized by increased cloudiness and precipitation accompanied by greater vertical mixing rather than by thermal stratification. One further advantage of CHL_s as a descriptor for temperate lakes is its high correlation with phosphorus loading (Oglesby 1977) and water transparency (Oglesby and Schaffner 1975) for lakes having low concentrations of inorganic suspended matter and humic colloids. As a result, summer phytoplankton standing crop can be estimated indirectly in some cases.

Annual primary productivity is the more meaningful of the two phytoplankton measures in terms of ecosystem function. Regretably, the different methods of measurement in common use variously approximate gross and net production, and there are still serious unresolved questions concerning techniques for generating and interpreting the data. For these reasons and because of the low temporal and spatial frequencies of measurement characteristics of most studies, estimates of 1° are likely to be relatively inaccurate.

Another source of probable error on several scores is difference in lake size. Ryder et al. (1974) note that it is now generally accepted that "small lakes are exploited more efficiently per unit surface area than large lakes when both are subjected to proportionately similar fishing effort." Thus, when comparing many lakes of diverse sizes, an "artificial" effect of A and/or $\bar{z}$ is superimposed on any influence these parameters may actually have on yields. Size also affects the dependence of fish productivity on primary production, since as size decreases the proportionate significance of allochthonous organic material, e.g. leaf litter, terrestrial insects, and waste discharges, increases. Such material is readily incorporated into food webs with subsequent increases in fish yield unrelated to 1°C and associated factors (e.g. Sorokin 1972; Mann 1972).

Phytoplankton, the MEI, and Fish Yields

Oglesby (1976) introduced limited evidence that fish yield from lakes is dependent upon primary productivity and that it may alternatively be described as a function of phytoplankton standing crops averaged over the summer. Statistical analysis of published data on fish yield and phytoplankton for a small but highly diverse group of lakes located throughout the northern hemisphere was used to derive formal expressions of these relations. Enough information has now been obtained on additional lakes to permit refinement of the initial equations, establishment of tentative boundary conditions, and estimation of efficiencies with which 1° is converted to fish yield in various lakes. Factors related to (and probably controlling) phytoplankton

standing crop and production are discussed in Oglesby (1977).

Table 1 contains data on 46 lakes which were used to derive the three fish-yield models discussed below. No estimates of variance in the parameters included in Table 1 were possible. A wide range of values for some parameters is reported for most of the Indian ponds and impoundments. These data were included in only one of the regression calculations (see below). In this case arithmetical averages of all available data were used.

Y–CHL$_a$ AND Y–1° MODELS

The log-log regression of fish yield on summer phytoplankton standing crop (Fig. 1) is described by

$$(1)\quad \log Y_f = -1.92 + 1.17 \log \mathrm{CHL}_a;\ n = 19;\ r^2 = 0.84$$

Of the two points that deviate most the uppermost one to the left of the regression line represents Lake Suwa, Japan. Its very short hydraulic retention time, 0.14 yr, suggests that standing crop may not be a good reflector of primary productivity for this system, since washout of phytoplankton becomes an appreciable factor and the greater the inflow of water relative to lake volume the greater the input of allochthonous material is likely to be. The second point, lowermost in Fig. 1 and to the right of the regression line, represents Lake Huron, which contains depleted stocks of those species having higher economic value due to overfishing and sea lamprey predation (Berst and Spangler 1972; Jensen 1976). Lake George, the only tropical system represented in Fig. 1, fits the regression well. Ganf (1974) has shown that this lake may be at about the level of standing crop where light becomes limiting to productivity.

Upon plotting fish yield as a function of phytoplankton productivity (Fig. 2) it became apparent that many of the smaller lakes deviated markedly from the pattern established by those of larger surface area. The following linear regression fits the log-log plot for lakes of $A > 10$ km^2 fairly well:

$$(2)\quad \log Y_{fc} = -6.00 + 2.00 \log 1°;\ n = 15;\ r^2 = 0.74$$

A slightly curvilinear function, with the rate of increase in yield decreasing at higher 1° values, would provide an even better fit to the data, but I have decided against such attempts at further refinement until more information is available.

The points represented by broken circles show the position on the graph of lakes of < 10 km^2 surface area. The two on the left are for Juiceys Pond and Forderer Finstertaler See, while those at the top of the figure show the relation to the regression of a carp pond in Israel (located to the left) and a composite (obtained by averaging all 1° and Y_{fc} data) representing 14 small Indian ponds and reservoirs.

Malack (1976) has developed two regressions, one

TABLE 1. Data on phytoplankton, fish yield, and morphoedaphic factors for lakes, ponds, and reservoirs located from the equator to north temperate latitudes.

Lake Name, Location (and Reference)	CHL_a (mg m^{-3})	1° (g C m^{-2} yr^{-1})	Y_f (g dry wt m^{-2} yr^{-1})	Y_{fc} (g C m^{-2} yr^{-1})	$\bar{z}$ (m)	A (m^2 x 10^{-6})	MEI$_{225}$ (TDS/$\bar{z}$)	(A/$\bar{z}$)
North America								
1. Athabasca Canada, 59°N (Rawson 1960)	2.2[a]	-	0.011	0.0044	26	7900	2.23	-
2. Crne Canada, 56°N (Rawson 1960)	1.1[a]	-	0.026	0.010	14.9	1152	1.81	-
3. Wollaston Canada, 58°N (Rawson 1960)	1.6[a]	-	0.030	0.012	20.6	2062	1.70	-
4. Reindeer Canada, 57°N (Rawson 1960)	1.6[a]	-	0.030	0.012	37+	5569	2.29	-
5. La Ronge Canada, 55°N (Rawson 1960; Ryder 1972)	0.2[a]	-	0.029	0.011	12.7	1176	11.7	7.64
6. Berrie Canada, 55°N (Rawson 1960)	4.1[a]	-	0.062	0.033	13.2	329	6.67	-
7. Churchill Canada, 56°N (Rawson 1960)	11.1[a]	-	0.085	0.034	9.0	433	15.1	-
8. Big Peter Pond Canada, 56°N (Rawson 1960)	9.5[a]	-	0.140	0.056	13.7	552	10.0	-
9. Little Peter Pond Canada, 56°N (Rawson 1960)	13.4[a]	-	0.168	0.067	5.1	184	26.2	-
10. Waskesiu Canada, 54°N (Rawson 1960)	6.0[a]	-	0.195	0.079	11.5	70	16.9	-
11. Juiceys Pond Canada, 48°N (Kerekes 1972)	2.2[b]	12.1[b]	0.065	0.026	-	-	-	-
12. Superior U.S.A.-Canada, 47°N (See Oglesby 1977; Lawrie and Rahrer 1972)	-	90	0.0092	0.0033	148	82417	2.06	3.36
13. Huron U.S.A.-Canada, 44°N (See Oglesby 1977)	2.5	65	0.0084	0.0034	60	59596	4.32	6.72
14. Michigan U.S.A., 42°N (See Oglesby 1977; Wells and Mclain 1972)	-	135	0.010	0.041	84	58016	4.72	9.24
15. Erie U.S.A.-Canada, 42°N (See Oglesby 1977; Leach and Nepszy 1976; Hartman 1972; Stu 1974)	-	245	0.022	0.009	10	25719	-	13.4
16. Ontario U.S.A.-Canada, 42°N (See Oglesby 1977; Christie 1972)	-	165	0.033	0.0048	40	19477	5.36	10.9
17. Oneida U.S.A., 43°N (See Oglesby 1977)	20.5	-	0.236	0.095	6.8	207	23.9	40.4
Great Britain								
18. Leven Scotland, 56°N (See Oglesby 1977; Thorpe 1974)	44	295	1.850	0.740	3.9	13.3	-	-
19. Neagh Northern Ireland, 55°N (See Oglesby 1977)	37	600	0.563	0.225	8.3	383	-	57.5
Europe								
20. Léman France-Switzerland, 46°N (Vivier 1975; Matthey 1975; Laurent 1972)	-	170	0.522	0.209	153	582	6.52	-
21. Maggiore Italy, 46°N (See Oglesby 1977)	-	290	3.429	0.172	177	212	-	5.40
22. Vorderer Finstertaler Austria, 47°N (See Oglesby 1977)	-	46	0.252	0.101	14.8	0.16	-	1.68
23. Tjeukemeer Res. Netherlands, 53°N (Beattie et al. 1972)	28	750	0.665	0.266	3.5	21	-	-
24. Kättern Sweden, 58°N (See Oglesby 1977)	2	-	0.0392	0.0157	39	1912	-	3.84
Africa								
25. George Uganda, 00°N (See Oglesby 1977; Gwahaba 1973)	189	-	4.25	1.70	2.25	250	-	66.9
Asia								
26. Unnamed carp pond Israel, 30-35°N? (Hepher 1962)	-	694[c]	25.0[c]	10.0[c]	0.7-0.9	0.001	-	-
27. Sevan U.S.S.R., 59°N (Moskalenko and Vittinyes 1972; Moskalenko 1972)	-	122.5	0.060	0.024	730	31500	-	4.00
28. Suwa Japan, 36°N (Sakamoto et al. 1975)	58	-	6.83	2.75	8.1	14.8	-	-
29. Nyampalan India, 10°N (See Oglesby 1977)	-	3295[d]	33.95	13.58	3	0.014	-	407
30. Kodaikanal India, 10°N (Oglesby 1977; Sreenivasan 1972)	-	146-164[d]	0.032-1.32	0.0129-0.530	2	0.24	-	73.5
31. Vercaud India, 12°N (Same as [30])	-	1058-1073[d]	0.752-55.90	0.301-22.0	2	0.08	-	66.0-100
32. Ooty India, 11°N (Same as [30])	-	1369-1386[d]	0.790-2.55	0.319-1.02	3	0.34	-	48.3-158
33a. Stanley Res. India, 12°N (Gunapati 1973)	-	711[d]	0.560	0.225	-	-	-	-
33b. Stanley Res. (Gunapati and Sreenivasan 1972)	-	388[f]	0.356-0.712	0.143-0.285	16.3	155.4	-	-
33c. Stanley Res. (Sreenivasan 1972)	-	644[d]	1.572	0.629	13	142	-	7.64-18.7
34. Fort Moat (C) India, 13°N (Same as [33b])	-	2964[f]	22.5-57.0	9.00-20.4	1	0.008	-	475-1150
35. K. C. Kalen India 13°N) (Same as [33b])	-	3275[f]	83.5-154.6	29.92-61.84	2	0.006	-	400-1000
36. Fort Moat (Sec. A) India, 13°N (Same as [33b])	-	3424[f]	56.5-123.2	22.6-49.3	1.5	0.014	-	750-1667
37. Fort Moat (Sec. B) India, 13°N (Same as [33b])	-	1988[f]	56.5-123.2	22.6-49.3	1	0.03	-	975-2909
38. Bhavanisagar Res. India, 11°30'N (Same as [33c])	-	950[d]	0.695	0.278	11.9	78.75	-	4.03-16.8
39. Sethanur Res. India, 12°N (Same as [33c])	-	964[d]	0.92	0.368	10.1	12.6	-	11.7-19.2
40. Krishnagiri Res. India, 12°30'N (Same as [33c])	-	580[d]	4.00	1.60	5.3	32.5	-	47.2-108
41. Mnerkeotha Res. India, 11°30'N (Same as [33c])	-	1175[d]	2.36	0.86	11.7	8.5	-	2.77-4.38
42. Sandynulla Res. India, 10°N (Same as [33c])	-	646[d]	40.2	16.1	10.3	2.6	-	6.61-27.2
43. Obathurti Tank India, 11°30'N (Same as [33c])	-	981[d]	16.0	14.4	1.5	0.73	-	257-350
44. Fort Moat (A) India, 13°N (Same as [33c])	-	2274[d]	0.512	0.205	1.5	0.048	-	666-1870
45. Nyamulan India, 12°N (Same as [33c])	-	3285[d]	1.135	0.454	3	0.014	-	297-633
46. Chetpet Swamp India, 13°N (Same as [33c])	-	2662[d]	3.20	1.28	1	0.030	-	850-2300

[a] Estimated from Secchi disc transparencies (see Oglesby and Schaffner 1975 for basis of calculations).
[b] For Pine Hill Pond which Kerekes (1972) states has similar productivity.
[c] For 240 days, pond drained for rest of year.
[d] Net production.
[e] Gross production.
[f] Not specified whether net or gross.

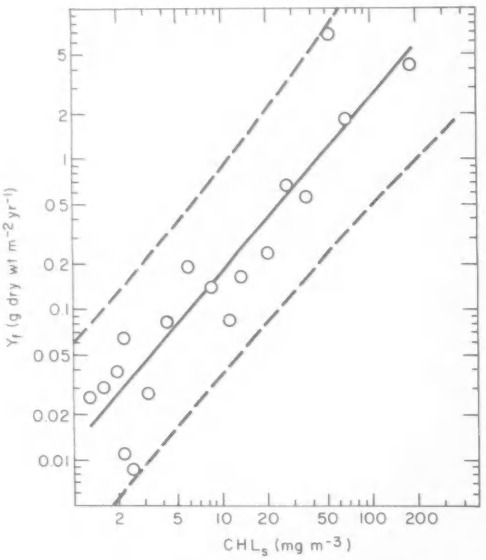

FIG. 1. Regression of fish yield on summer phytoplankton standing crop for 19 lakes; 95% confidence intervals for predicting values about the mean are within the dashed lines.

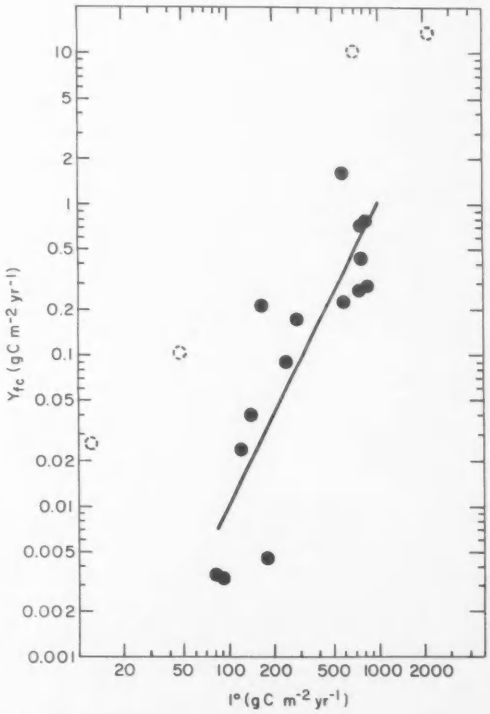

FIG. 2. Regression of fish yield on annual primary productivity for 15 lakes of A > 10 km^2 (●). Smaller lakes (○) (see text).

for 8 African lakes and another for 15 Indian lakes, expressing fish yield as a function of gross (oxygen evolution) primary production. A rough conversion of his 1° estimates to comparable ^{14}C uptake values (Table 1) indicates a reasonable fit of the African lakes to an extrapolation of the regression shown in Fig. 2. The Indian lakes he refers to are essentially the same as those summarized by the top broken circle in Fig. 2.

EFFICIENCY OF YIELD

The efficiency with which carbon is transferred to fish yield can be estimated for those lakes where primary productivity is known. When this is done, five fairly distinct classes of lakes can be differentiated (Table 2).

Class I consists of small ponds and reservoirs located in the subtropics. The carp pond in Israel was designed and managed to maximize yield. Stocking with young carp eliminated the reproductive costs of producing fish in this system, and it is presumed that at the end of the 240-day growing period all fish were harvested. No data were available on the management of the Indian ponds and reservoirs. Some were probably stocked and at least the smaller bodies of water were most likely harvested with high efficiency. Some of these are known to receive considerable allochthonous organic material in the form of sewage, so that not all of the fish production is dependent upon carbon fixed by photosynthesis. Efficiencies for the individual Indian systems were characterized by extremely high variability between systems and between years for a given pond or reservoir.

The only properties that Class II lakes have in common with those in Class I appear to be their small size, and to a lesser extent, their shallowness. Factors that may uniquely contribute to the high efficiencies for Vorderer Finstertaler and Juiceys Pond are the restricted number of top carnivore species, the probable completeness with which catch is assessed in the case of the former, and the fact that Y_{fc} for Juiceys Pond represents an estimate of maximum sustainable production.

Classes III and IV contain a wide variety of lakes ranging from shallow to very deep, of moderate to very large surface areas, and of moderate to high productivities. Those for which information was available all have a history of supporting well-developed fisheries. At least some of these lakes are in a state of biological change due to increasing 1°, e.g. Maggiore, and/or shifts in fish populations due in part to past overexploitation of some species, e.g. Michigan and Erie.

TABLE 2. Rank order of carbon transfer efficiency from phytoplankton primary production to fish yield and pertinent characteristics of lakes and their fisheries.

Lake(s)	Efficiency (Y_{fc}:1° × 100)	Class	Characteristics
Israel carp pond	1.49	Class I, very high efficiencies	Small, shallow, tropical to subtropical, most are highly eutrophic, probably high percentage harvest of annual fish production
14 Indian ponds and reservoirs of $A < 10$ km² (avg)	0.68 0.68		
Vorderer Finstertaler	0.21	Class II, high efficiencies	Small, shallow to moderate $\bar{z}$, temperate, very low 1°, only 2 species of top carnivores noted for each, salmonid sport fisheries
Juiceys Pond[a]	0.21		
Léman	0.12	Class III, moderate efficiencies	Moderate to large A, shallow to deep tropical to temperate, moderate to high 1°; Léman and Leven have long histories of well-developed fisheries
4 Indian reservoirs of $A > 10$ km² (avg)	0.11		
Leven	0.09		
Maggiore	0.06	Class IV, low efficiencies	Moderate to very large A, shallow to very deep, temperate, moderate to high 1°, generally long history of well-developed fisheries, overexploitation of some species in past for at least some of these lakes
Neagh	0.04		
Erie	0.04		
Tjeukemeer Res.	0.04		
Michigan	0.03		
Baikal	0.02		
Huron	0.004	Class V, very low efficiencies	Very large, very deep, temperate, low to moderate 1°, long history of well-developed fisheries, overexploitation of some stocks in the past
Superior	0.004		
Ontario	0.002		

[a] Y_{fc} for this pond represents an estimate of maximum sustainable yield.

Class V represent three very large, deep, cold-water lakes of low to moderate primary productivity. They overlap with the last two lakes listed in Class IV in every characteristic except efficiency and resemble Lac Léman and Lago Maggiore in many ways. The reasons for efficiencies of Class V lakes being 1–2 orders of magnitude lower than other lakes are not fully apparent, although Huron and Ontario, and to a limited extent Superior, have fisheries that are restricted because of earlier extirpation of commercially desirable species.

In comparing carbon transfer efficiencies it is important to realize that as computed these do not necessarily represent true biological efficiencies. Fishery management practices, the completeness with which catch is determined, inputs of allochthonous material to food webs, and the accuracy with which yields and primary productivities are measured all effect calculations. Taken together these factors result in inflating values obtained for Classes I and II relative to transfer efficiencies for other lakes.

Y–MEI MODELS

The morphoedaphic index (MEI) is an empirically derived expression used by Ryder (1965) to predict fish yield in unexploited Canadian lakes. It was proposed by Ryder et al. (1974) that its application may have more universality and Welcomme (1976) has successfully used various morphoedaphic factors to estimate Y for African rivers.

Oglesby (1976) has argued that the rational basis for relating the MEI (in its simplest TDS/$\bar{z}$ or $\lambda/\bar{z}$ form) to fish yield, namely that it is broadly indicative of nutrient inputs to lakes and their capacity to respond to such inputs as reflected by mean depth, makes the extension of the MEI to include culturally influenced lakes of doubtful validity and that considerable error may be introduced even in natural systems due to variations in geochemical ratios of phosphorus to other elements.

On the other hand, the morphoedaphic index has two very important virtues, its extreme simplicity and the fact that data needed are widely available or readily determinable by simple methodologies. The MEI can be calculated as the ratio of either total dissolved solids or conductivity to mean depth. As was found with the relation of phytoplankton standing crops and productivity to the MEI, a preliminary analysis of the data in Table 1 indicated that mean depth ceased to be relevant when greater than about 25 m (Oglesby 1977), and so this was taken as the upper limit of $\bar{z}$ used in the calculations. Fish yield as a function of $MEI_{\bar{z}25}$ is shown in Fig. 3.

Of the 17 lakes included in Fig. 3a, 12 are only slightly influenced by human activities and none are severely affected by discharges of wastes. All are

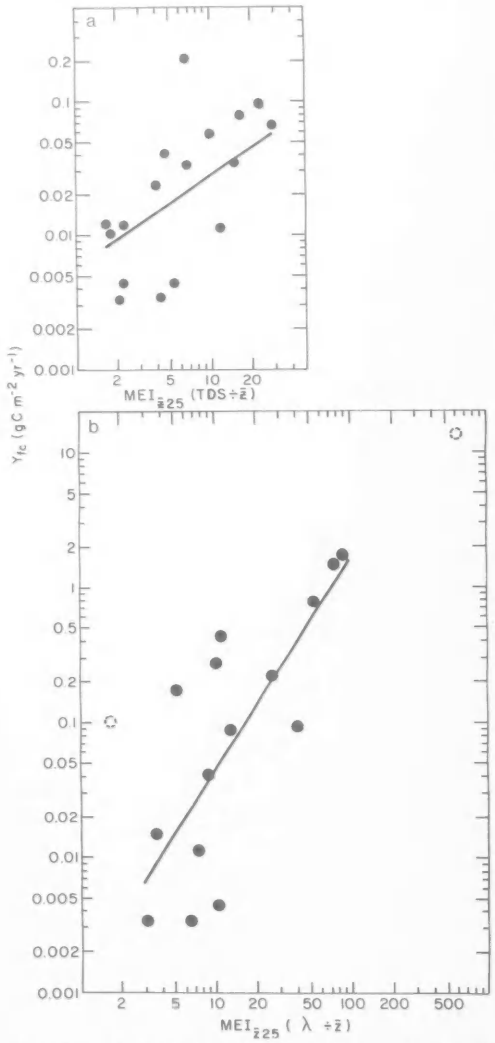

FIG. 3. a, Fish yield as a function of the morphoedaphic index (TDS/$\bar{z}$) for 17 large lakes; b, regression of fish yield on the morphoedaphic index (λ/$\bar{z}$) for 15 lakes of $A > 10$ km (●). Smaller lakes (○) (see text).

large and the Laurentian Great Lakes and Baikal are very deep. The regression is significant at $\alpha = 0.01$ and is represented by

(3) $\log Y_{fc} = -2.24 + 0.69 \log x$; $n = 17$; $r^2 = 0.38$

where $x = \text{MEI}_{\bar{z}25}(\text{TDS}/\bar{z})$.

The lakes shown in Fig. 3b span a much wider range of MEI and yield values. The regression line represents only those lakes with $A > 10$ km^2. Note the similarity of point distribution to that of Fig. 2 but the slightly larger scatter. The regression shown in Fig. 3b is represented by

(4) $\log Y_{fc} = -2.91 + 1.56 \log x$; $n = 15$; $r^2 = 0.59$

where $x = \text{MEI}_{\bar{z}25}(\lambda/\bar{z})$. When the average of all $\text{MEI}_{\bar{z}25}$ and Y_{fc} values for 14 small Indian ponds and reservoirs is included the regression becomes

(5) $\log Y_{fc} = -2.81 + 1.47 \log x$; $n = 16$; $r^2 = 0.70$

While these small subtropical systems may closely fit the relation obtained for larger temperate lakes when considered as an aggregate, their great variability (between systems and between years) negates the possibility of developing a predictive relation applicable to individual ponds or reservoirs.

Boundary Conditions for Models

A review of Fig. 2 and 3 indicates that some lakes do not fit the general patterns established for the majority. If such lack of fit can be explained, a logical basis can be established for excluding inappropriate systems, i.e. boundary conditions can be determined for the various models.

Lakes of surface area $\lesssim 10$ km^2 do not conform well to the regressions expressed by Equations 2–4. In all probability this is due to a combination of greater harvesting efficiency in small systems (Ryder et al. 1974); the increased importance of allochthonous organic imputs into such lakes, e.g. Lake Tatsu-Numa, Japan (Yamamoto 1972); the increased efficiency with which total catch is estimated; and in cases such as fish culture ponds, intensive management practices like complete removal of fish at short intervals followed by restocking with juveniles. Fish yields from small lakes also appear to be much more variable from year to year than do those for larger bodies of water. For all of these reasons equations for predicting the yields of fisheries in small systems are likely to be developable only for purposes of comparing sets of lakes that differ substantially in only one of the above variables. Therefore, lakes of $A \leq 10$ km^2 are excluded from the Y_{fc}–1° and Y_{fc}–MEI models and probably should not be included in the Y_f–CHL_s model, although case history evidence on this point is lacking.

Of the above factors, the influence of allochthonous organic material seems most likely to cause deviation from the Y-phytoplankton regressions developed for larger lakes. For example, Rybinsk Reservoir ($A = 4550$ km^2) in the USSR is described as receiving organic material from external sources to such an extent that 1° accounts for only 25% of the reduced carbon entering the base of the food chains (Sorokin 1972). When this is allowed for, average supply of carbon to the food web base becomes about 260 mg·m^{-2}·yr^{-1} and the comparable Y_{fc} value is about 90 mg C·m^{-2}·yr^{-1}, which fits Equa-

tion 2 very closely. Thus, lakes receiving substantial organic inputs in relation to that produced autochthonously should be excluded from the models unless a correction can be made to allow for these. In the case of discharges from sewage treatment plants this should be easy to do, since flow and biochemical oxygen demand (BOD) are routinely measured in most cases, and this data can be readily converted to an estimate of reduced carbon from C:O ratios.

Lakes with mean hydraulic retention times $\lesssim 0.4$ yr should be excluded from the Y_f–CHL_s model. The fact that Lake Suwa ($\tau_\omega = 0.14$ yr) deviates from the regression by substantially exceeding the expected fish yield provides some confirmatory evidence that very high flushing rates may change the relation of CHL_s to 1° and hence make the former inapplicable to the model. Hydraulic retention time data were not available for some of the lakes in Table 1. However, where known, τ_ω ranged (with Suwa excepted) from 0.43 yr (Leven) to 182 yr (Superior) with no apparent effect on the fish-yield regressions.

Another condition for which the Y_f–CHL_s model is not rationally applicable is that of tropical lakes. The fact that Lake George fits this regression may be the result of a low photosynthetic efficiency (ratio of carbon produced to chlorophyll concentration). If Lake George approximates an upper limit of primary production (Ganf 1974), it may also represent the upper boundary of fish production to be expected from large, shallow lakes not subject to intensive management. This might help explain its fit to Equation 1. At any rate, the Y_f–CHL_s model should not be applied to tropical lakes until further examples can be studied.

Lakes representative of two other situations should be excluded from both phytoplankton and MEI models of yield. These are lakes where fish growth or survival are significantly influenced by toxic materials and those where macrophytes and/or epiphytes contribute a high percentage of total 1°. Neither situation can be defined with any exactitude. The former must include not only cases where well-recognized toxicants are involved but also instances where environments have gradually become hostile to fish through long-term inputs of materials that act cumulatively, for example some lakes in southeastern Ontario (Beamish 1974, 1975) and Scandinavia that have been acidified by atmospheric fallout.

One of the restrictions that Ryder et al. (1974) imposed on data sets to be included in their Y–MEI models was relative homogeniety of climate. Regier et al. (1971), as cited by Ryder et al. 1974, reported what appeared to be a large influence of latitude on fish yield. No such effect was apparent for data used in the present study. Since the presumed action of latitude is chiefly that of determining light available for photosynthesis, the finding that light significantly influenced CHL_s and 1° for a large group of lakes only when at very low levels (Oglesby 1977) is in agreement with the lack of effects observed for fish yield. At any rate, as biological responses to light, if any, are already accounted for in the CHL_s and 1° expressions, latitude can be ignored as a variable relating to the Y-phytoplankton models. Allowance may have to be made in the Y_{fc}–MEI regression for very low-incident light conditions and for circumstances where light might be limiting due to its reduced penetration in the water column.

Predictability of Fish Yield

For purposes of fishery management, data on yield, phytoplankton production, and standing crop, and the abiotic properties of lakes may be usefully viewed in a generalized format; this is presented as an expectation-variability diagram (ACMRR/IABO 1976) in Fig. 4. The relative positions, subjectively determined, of most of the lakes included in the models are shown. The purpose of this diagram is to give an overview of the consequences of interactions by the variables and so no attempt has been made to scale the axes.

Figure 4 shows that expectation of yield increases as primary productivity increases and that surface area has little effect until lakes reach a certain minimum size (on the order of 10 km² or less) at which point Y becomes greater as A decreases. Similarly, depth has little effect until $\bar{z}$ becomes $\lesssim 25$ m, at which point yield increases as a function of decreasing depth. The relation of dissolved solids con-

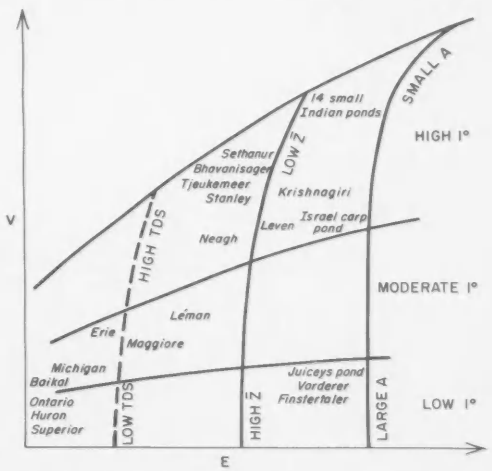

FIG. 4. Relation of expectation (E) and variability (V) of fish yield to lake productivity and several morphoedaphic properties. Approximate positions on the E–V diagram of most of the lakes used to derive the yield models are shown.

centration to Y is indirect and less certain. The variability component of Fig. 4 indicates that this management parameter is higher for the more productive lakes and for those that are smaller and shallower.

Variability should of course decrease and expected yield increase as a function of how intensely proper management techniques are applied. Since biotic and abiotic factors are inherently more controllable in small compared with large lakes, it is the former that offer the best prospects for obtaining high sustainable yields.

The principal value in expectation-variability diagrams is their use in the strategic and tactical planning of fishery research. Another need of fishery managers is for methods to reliably estimate potential fish yield for a particular body of water or for those in a given region. The relations established between Y and CHL_s, 1° and MEI show considerable promise of being useful in this regard, especially when sets of lakes are to be considered.

For the variables tested, the highest correlation of fish yield was that with CHL_s (Fig. 1 and Equation 1). Lakes represented in this regression range from oligotrophic to highly eutrophic, small to very large in area, and very shallow to very deep. Types not represented include those that are very small but deep, those that are very large and very shallow, and those that are very large and very high in TDS. Predictions made within the present 95% confidence intervals reduce the range of potential yields from a possible span of about 10,000 to 25.

Of more interest to ecologists is the relation of fish yield to primary production. However, more research is needed before this is ready as a predictive tool. Points that need to be clarified include better defined boundary conditions and the probability that this function is curvilinear (with important implications for fishery management). Despite these limitations, the relation shown in Fig. 2 confirms the generality that fish yield is highly dependent upon input at the lowest trophic level and indicates that this may hold over a range of about 3.5 orders of magnitude of Y_{fc} and 2 orders of magnitude of 1°.

The MEI, CHL_s, and 1° all appear to be useful estimators of fish yield from lakes. Logic dictates that the two biotic parameters should provide more reliable predictions but that availability of morphoedaphic data will be greater. This dichotomy suggests that additional research employing one or a combination of any of these as potential fish yield correlates will produce worthwhile results. More and better information is needed if sources of variance are to be identified and quantified.

Management Applications

Use of the kind of information presented in this paper for developing fishery management tactics and strategy would involve the following sequence of actions. First, an expectation-variability diagram might be used to gain a general perception of the nature of fisheries in the lake(s) being considered and the kinds of results to be expected from a program of research and management. Second, the suitability of using one or more of the various regressions as predictors for the particular situation must be determined. A given lake or lakes must first conform to boundary conditions, and then applicability of a particular model is judged from the kinds and amount of data available or that can be gathered. Third, where appropriate, a regression or regressions is (are) used to predict a range of yields. Finally, regulations are set that conform to patterns already proved successful for other lakes having histories of sustained yields in the same range predicted for the systems under study.

The foregoing scheme of management-related activities is suggested as a supplement to, not a replacement of, presently used approaches. Many finer points, important for the management of any particular lake or set of lakes, have been ignored as have some of the basic ecological considerations. The reader is particularly referred to Regier and Henderson (1973) and ACMRR/IABO (1976) for a more complete description of frameworks into which the foregoing suggestions for fishery management might be fitted.

Acknowledgments

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Vertical and Seasonal Distribution of Chlorophyll *a* in Lake Michigan[1]

ARTHUR S. BROOKS AND BYRON G. TORKE[2]

Department of Zoology and Center for Great Lakes Studies, The University of Wisconsin-Milwaukee, Milwaukee, Wis. 53201, USA

BROOKS, A. S., AND B. G. TORKE. 1977. Vertical and seasonal distribution of chlorophyll *a* in Lake Michigan. J. Fish. Res. Board Can. 34: 2280–2287.

Vertical and seasonal distribution of chlorophyll *a* was observed for 2 yr at an offshore station in Lake Michigan. Chlorophyll *a* concentrations increased uniformly at all depths during spring reaching 3–4 mg/m³ by late May. Thermal stratification was followed by development of a subthermocline chlorophyll peak between 10 and 30 m that reached 8.5 mg/m³ by late July. The major subthermocline peak collapsed in mid-August but was followed by two lesser peaks at depths of 10 and 30 m. Autumn mixing dispersed these peaks in the mixed layer, increasing the chlorophyll content of the epilimnion at a time when integral chlorophyll levels were declining. At fall overturn chlorophyll concentrations were uniformly distributed at approximately 1 mg/m³, where they remained throughout the winter. The presence of a deep chlorophyll maximum in Lake Michigan adds a new dimension to limnological studies of the Great Lakes. The influence of this peak must be considered in future investigations of food chain dynamics and eutrophication processes in the Great Lakes system.

Key words: Laurentian Great Lakes, limnology, chlorophyll *a*, spatial distribution, phytoplankton dynamics

BROOKS, A. S., AND B. G. TORKE. 1977. Vertical and seasonal distribution of chlorophyll *a* in Lake Michigan. J. Fish. Res. Board Can. 34: 2280–2287.

Nous avons suivi la distribution verticale et saisonnière de la chlorophylle *a* pendant 2 ans à une station du large dans le lac Michigan. Les teneurs en chlorophylle *a* augmentent uniformément à toutes les profondeurs au printemps et atteignent un maximum de 3–4 mg/m³ fin mai. La stratification thermique est suivie de la formation, entre 10 et 30 m, d'un pic de chlorophylle sous la thermocline, atteignant des teneurs allant jusqu'à 8.5 mg/m³ fin juillet. Le pic principal de la sous-thermocline disparaît à la mi-août mais est suivi de deux pics moins importants aux profondeurs de 10 et 30 m. La circulation automnale entraîne la disparition de ces pics dans la couche mélangée et une augmentation de la teneur en chlorophylle de l'épilimnion au moment où les niveaux de chlorophylle totale diminuent. Lors de la circulation automnale, les teneurs sont uniformément réparties à environ 1 mg/m³, niveau auquel elles demeurent durant tout l'hiver. La présence d'un maximum de chlorophylle en profondeur dans le lac Michigan ajoute une nouvelle dimension aux études limnologiques des Grands lacs. On devra tenir compte de l'influence de ce pic dans l'investigation future de la dynamique des chaînes alimentaires et du processus d'eutrophisation dans le réseau des Grands lacs.

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VERTICAL distribution of chlorophyll *a* in marine environments has been the subject of numerous investigations over a period of several years (Steele and Yentsch 1960; Anderson 1969; Hobson and Lorenzen 1972; Venrick et al. 1973). In freshwater systems, however, detailed studies of chlorophyll *a* profiles have only recently been undertaken (Berman 1972; Kiefer et al. 1972; Fee 1976).

Chlorophyll *a* studies on the Laurentian Great Lakes have mainly been concerned with the surface waters (Vollenweider et al. 1974). Relatively few studies have investigated the vertical distribution of chlorophyll *a* (Olson and Odlaug 1966; Putnam and Olson 1966; Munawar et al. 1974; Stadelmann and Fraser 1974; Watson et al. 1975) and these have been limited to summer sampling or to a restricted portion of the water column.

The present study was undertaken to investigate the vertical distribution of chlorophyll *a* at a deep station in Lake Michigan over a period of 2 yr.

[1]Contribution No. 153, Center for Great Lakes Studies, The University of Wisconsin-Milwaukee, Milwaukee, Wis. 53201, USA.

[2]Present address (B.G.T.): Department of Biology, Ball State University, Muncie, Ind.

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Materials and Methods

Samples were collected from the R.V. *Neeskay* at a 140-m deep station in Lake Michigan, 43°21′24″ N, 87°35′25″ W. Forty-five cruises were made at approximately biweekly intervals March 1973–December 1974. Additional sampling was conducted at deep stations in the north and south basins of the lake, July 10 and 15, 1974. Depths and coordinates were 240 m, 44°16′48″ N, 87°07′00″ W, and 130 m, 43°46′10″ W, 87°09′00″ W, respectively.

All collections were made between 1100 and 1400 h CST. Temperature profiles were taken by bathythermograph. Light penetration was determined by Secchi disc. Water samples were taken with a 9-ℓ opaque PCV van Dorn bottle from depths of 0, 2, 5, 10, 15, 20, 30, 45, 65, 85, 105, and 130 m on the first 10 cruises with 25 and 35 m depths added for the remainder of the study.

A 1-ℓ subsample for chlorophyll analysis was passed through a 250 μm Nitex screen to remove large zooplankters and filtered through a 0.45 μm Whatman GF/C glass fiber filter saturated with $MgCO_3$. Grinding and extraction procedures were those recommended by Strickland and Parsons (1972). The concentrations of chlorophyll *a* and phaeophytin *a* were determined using a Turner model 111 fluorometer calibrated with extracts of chlorophyll from log-phase cultures of *Fragelaria crotonensis* (Strickland and Parsons 1972). Phaeophytin *a* was subtracted from the chlorophyll *a* values to yield corrected values which are reported here. Subsamples for phytoplankton analysis were preserved with Lugol's solution, concentrated tenfold by settling and counted in Palmer chambers at 250× magnification on a Leitz upright compound microscope. Specific identifications were made on standard microscope slides at 1000 × magnification.

Results

During winter, December–March, water temperature and chlorophyll *a* profiles exhibited uniformly low values throughout the water column (Fig. 1). Temperatures decreased below 4°C at all depths indicating complete vertical mixing. Occasionally temperatures 10–20 m above the bottom were up to 1°C warmer than those in the upper portion of the water column, and a slight decrease in chlorophyll *a* concentration was noted within this stratum.

The spring phytoplankton increase in Lake Michigan began in mid- to late winter as shown by the gradual increase in chlorophyll *a* at all depths during January and February (Fig. 1). The major phytoplankton pulse did not commence until late March. Chlorophyll *a* values and temperature increased uniformly at all depths through April and May, reflecting the influence of increased solar input and continued vertical mixing. Maximum chlorophyll *a* concentrations of 3–4 mg/m³ were attained at all depths by late May to early June as temperatures reached 5–6°C and thermal stratification developed.

The establishment of thermal stratification in mid- to late June produced a dramatic change in the chlorophyll *a* profile (Fig. 1). Surface and bottom chlorophyll *a* concentrations decreased abruptly as a peak appeared between 10 and 30 m, just beneath the developing thermocline. As surface temperatures increased through June and July the thermocline became well established. Surface and bottom chlorophyll *a* concentrations decreased below 1.0 mg/m³ while the chlorophyll peak intensified between 10 and 50 m. The maximum chlorophyll values observed in the peak were 8.5 mg/m³ at a depth of 25 m on July 30, 1973, and 5.5 mg/m³ at 15 m on July 23, 1974. The actual maximum values and the shape of the chlorophyll profiles may vary somewhat from those illustrated, since the data were derived from discrete samples taken at specific depths. Chlorophyll *a* concentrations in the hypolimnion, below the depth of the peak, remained low through August, while a gradual increase in surface chlorophyll values was observed. Chlorophyll *a* concentrations in the peak decreased during early August and by mid- to late August a distinct chlorophyll maximum was no longer evident.

Following the breakdown of the major subthermocline chlorophyll maxima, two separate peaks formed in both 1973 and 1974. The uppermost peak developed at a depth of 10 m in close association with the thermocline. Epilimnetic chlorophyll concentrations gradually increased as this peak developed. The second peak was situated, as was the earlier major summer peak, beneath the thermocline at a depth of 30 m. Both peaks intensified during early September but did not attain chlorophyll levels >3.5 mg/m³. Surface cooling and mixing commenced during late August and early September, causing the thermocline to gradually descend, thickening the surface-mixed layer. As this occurred the two chlorophyll peaks were dispersed, causing a slight increase in chlorophyll levels in the mixed layer. During this period hypolimnetic chlorophyll concentrations declined to <0.5 mg/m³.

Through the remainder of the fall chlorophyll *a* values in the hypolimnion declined further toward their annual minimum. Epilimnetic values stabilized and remained between 1 and 2 mg/m³ through November. The effects of cooling and mixing were dramatically illustrated during this period as the thermocline descended rapidly, greatly increasing the extent of the mixed layer. The chlorophyll *a* and temperature profiles were nearly identical during this period. As the last vestige of the thermocline disappeared and complete mixing again occurred, the chlorophyll *a* in the water column was homogeneously distributed from top to bottom at a concentration of about 1 mg/m³. As the water continued to cool and mix through the winter, chlorophyll *a* levels remained relatively constant until the spring increase began anew.

The presence of a deep chlorophyll maximum in Lake Michigan appears to be a widespread phenom-

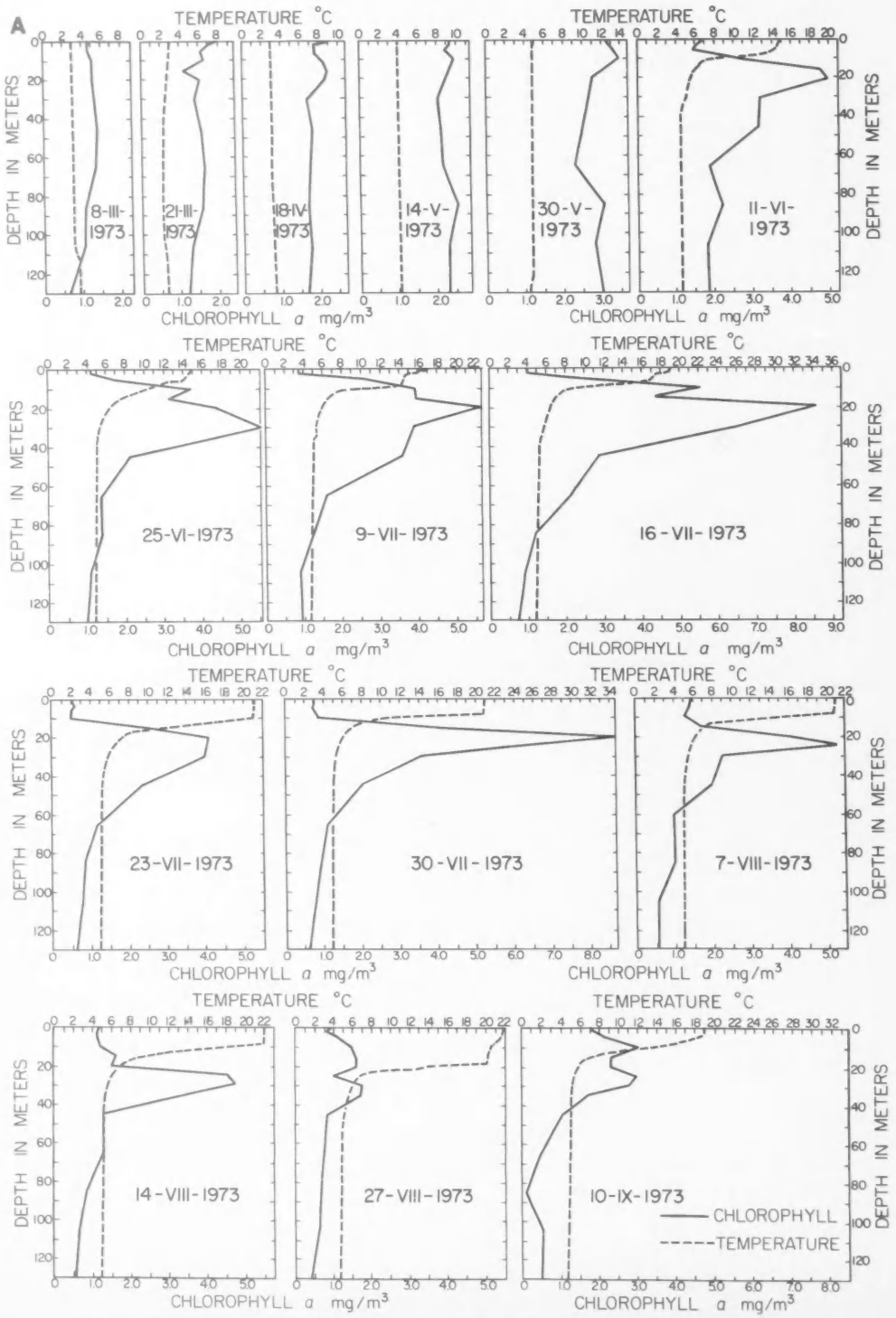

FIG. 1. Temperature and chlorophyll *a* profiles from the principal sampling station in Lake Michigan.

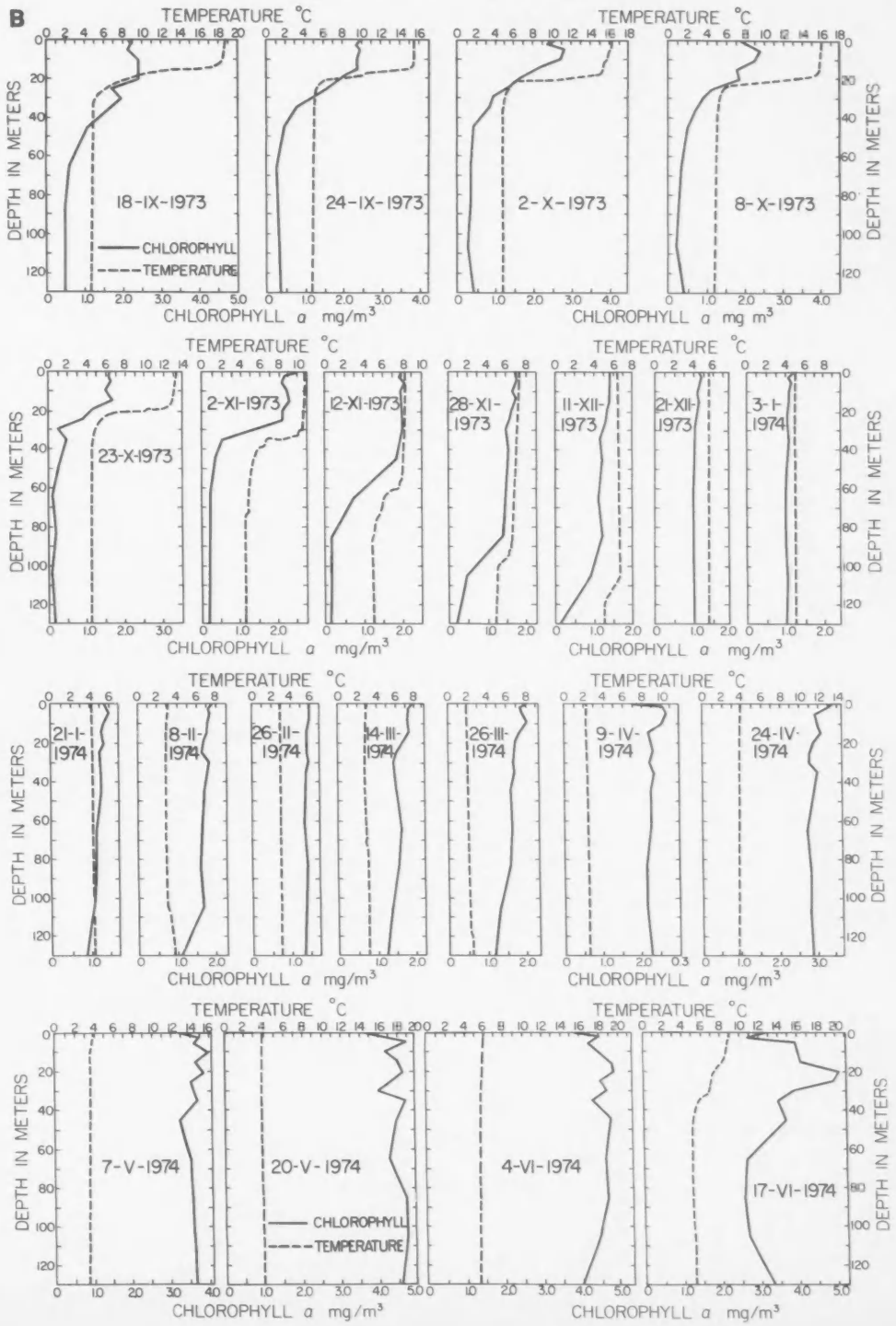

FIG. 1. *Continued.*

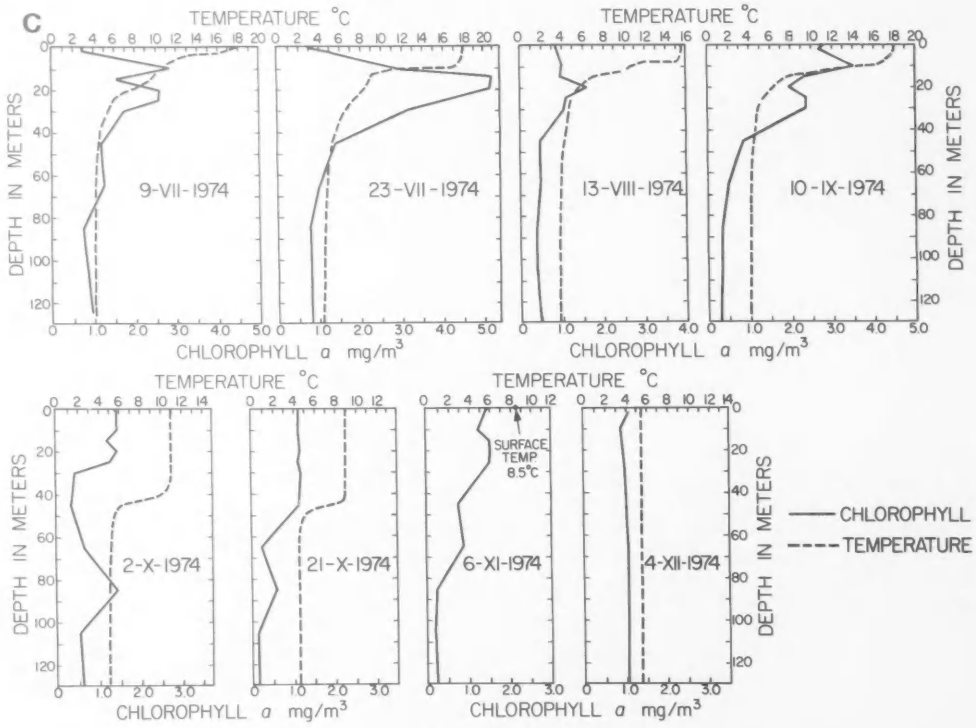

FIG. 1. *Concluded.*

enon during periods of thermal stratification. Observations made in the northern and southern basins of the lake in July 1974 indicate that the chlorophyll *a* profiles described above for the primary sampling station are typical of offshore Lake Michigan waters.

An examination of the total amount of chlorophyll *a* in the water column at the primary sampling station provides additional insight to the seasonal phytoplankton cycle in Lake Michigan (Fig. 2). The gradual increase in chlorophyll *a* content, which occurred through January and February 1974, is well illustrated in this figure as is the initiation and development of the major spring bloom. The greatest phytoplankton biomass, expressed as chlorophyll *a*, was observed during May and June in 1973 and 1974. Maximum integral values observed were 325.0 and 546.0 mg/m² for 1973 and 1974, respectively.

A sharp decline in total chlorophyll *a* was observed in late June. A secondary peak, which appeared in July 1973, and a lesser shoulder, noted in 1974, coincided with the maximum development of the subthermocline chlorophyll peak. Minimal biomass values were reached in mid- to late August as the deep chlorophyll peak began to collapse. A slight pulse was observed in early September as the two secondary peaks developed. The minimum integral chlorophyll value for the year of 39.0 mg/m² was reached in late October in 1973. The fall minimum of 84.5 mg/m² observed in 1974 was approximately equal to the absolute seasonal minimum of 78.0 mg/m², which was observed earlier in August. An increase in chlorophyll was observed in November of 1973 and 1974 as complete vertical mixing was approached. This increase raised the mean integral chlorophyll *a* concentration to levels that remained relatively constant through the winter.

Observations of the dominant phytoplankton species are presented to shed light on the dynamics of the chlorophyll *a* profiles described above. In 1973 and 1974 the spring bloom in Lake Michigan was dominated by *Melosira italica* and *M. islandica*. Once thermal stratification became established in June, *Melosira* spp. disappeared from the surface waters. For the remainder of the summer the phytoplankton community in the epilimnion was dominated by *Tabellaria fenestrata*, *Dinobryon sociale*, and numerous green and blue-green species. The community in the region of the chlorophyll peak was composed of *D. sociale*, *T. fenestrata*, *Fragellaria crotonensis*, green and blue-green filaments, and several small green species. Beneath the chlorophyll

FIG. 2. Integral chlorophyll *a* concentration vs. time at the principal sampling station in Lake Michigan.

peak the hypolimnetic phytoplankton community was composed of *M. italica* and *M. islandica*, with some *T. fenestrata* appearing in the upper part of this zone. In early fall as thermal stratification began to break down, the surface phytoplankton continued to be dominated by *T. fenestrata*, although a *Rhodomonas* sp. appeared at this time and gradually replaced *T. fenestrata* as the most abundant epilimnetic form by late fall. Other species of significance observed in the mixed layer during the fall included *F. crotonensis*, *Lyngbya* sp., and other filamentous blue-greens. The hypolimnetic community continued to be dominated by *M. italica*, while more *T. fenestrata* and *F. crotonensis* appeared in the bottom waters as the season progressed. Through November and December as temperatures continued to fall and mixing eroded more of the hypolimnion, the winter diatom community began a resurgence. Following the overturn and a return to homothermal conditions, *M. italica* once again became the dominant phytoplankton species.

Discussion

Winter Conditions

The low chlorophyll *a* concentrations we observed during the winter are similar to surface values observed by Rousar (1973) and concur with the low diatom counts reported by Holland and Beeton (1972). The uniform vertical profiles for temperature and chlorophyll *a* indicate that complete vertical mixing occurs at this station. However, the occasional occurrence of warmer temperatures and lower chlorophyll *a* concentrations in the bottom 10–20 m suggests that during calm periods mixing fails to reach the bottom strata of the lake. The warmer temperatures and lower chlorophyll values may be caused either by the advection of water masses with differing physical properties into the bottom layers or by the confinement of the bottom waters and the algae contained therein to a dark region of reduced turbulence, isolated from surface cooling and light.

Vernal Increase

Stoermer and Kopczynska (1967) concluded that the spring diatom bloom in Lake Michigan originates in nearshore waters and spreads offshore following the advance of thermal contours. A similar phenomena was also observed in Lake Ontario with the lakeward progression of the spring thermal bar (Lorefice and Munawar 1974). Although this may be true of nearshore waters, our observations offshore indicate that the spring diatom increase commences in late winter, while the initiation of major bloom coincides with the rapid rise of solar input during late March, consistent with the information presented by Hutchinson (1967) and Pechlaner (1970). Increases in temperature and/or nutrients were not directly involved in the initiation of the pulse, since temperatures remained between 2 and 3°C during this period, eliminating the influence of rising temperatures or the thermal bar from consideration, and there was no sudden spring overturn in Lake Michigan to rapidly elevate the concentration of nutrients. Nutrient concentrations in the surface waters of the lake have been shown to remain at high levels throughout the winter, with no marked increase in the spring (Rousar 1973; Mortonson 1977).

The maximum chlorophyll concentration attained in the spring bloom of 1974 was nearly 40% greater than that observed in 1973. In spring 1973 the bloom was observed to peak in late May to early June as thermal stratification became established. The development of thermal stratification appears to have brought about physical conditions unfavorable for the continued growth of the spring diatom community. This observation concurs with those of Lund (1954, 1955) and the work discussed by Hutchinson (1967), which indicate that *Melosira* spp. sink from the surface waters as the epilimnion warms, thermal stratification develops, and vertical mixing becomes restricted.

During spring 1974 strong winds prevailed in early June preventing thermal stratification from becoming firmly established until late June, at least 2 wk later than in 1973. The maximum integral chlorophyll concentration occurred while full circulation was in progress. The decline following the peak in 1974 appears to conform to the classic picture of silica depletion (Lund 1950a, b; Parker et al. 1977) that leads to the collapse of the spring diatom community. Although no nutrient data were collected on our cruises, Rousar (1973), Parker et al. (1977), and Mortonson (1977) describe a decline in silica concentrations in Lake Michigan during spring, which reach limiting values in June. Silica data obtained from the city of Milwaukee water intake show a similar pattern in 1973 and 1974. The

silica values observed at Milwaukee during spring 1973 and 1974 were nearly identical, supporting the hypothesis that the 1973 bloom was terminated by the early onset of stratification rather than nutrient limitation.

In light of these observations the termination of the spring diatom bloom in Lake Michigan is apparently brought about either by nutrient depletion in the fully mixed column, as suggested by the 1974 data, or by the development of thermal stratification, which may be inferred from the 1973 observations. In any particular year the exact mechanism that ends the bloom appears to be dependent on meteorological conditions during late spring. Mortonson (1977) arrived at a similar conclusion, which was supported by direct nutrient observations in comparing the spring blooms of 1975 and 1976.

Subthermocline Peak

The formation of the subthermocline chlorophyll peak in Lake Michigan may be explained according to two current hypotheses: the settling hypothesis of Steele and Yentsch (1960) and the more recent theory of in situ growth (Ichimura et al. 1968; Anderson 1969; Fee 1976). The physical–chemical conditions that existed in the lake at the time and depth of peak formation make the application of both theories plausible. The strata in which the chlorophyll maximum developed in Lake Michigan was a zone of reduced turbulence (Mortimer 1974), and increased nutrient concentrations (Schelske and Callender 1970; Mortonson 1977), conditions necessary for the settling theory to function. Light levels in the upper portion of the chlorophyll maximum zone were within the range of 0.1–1.0% of surface values, a range which has been reported in association with in-situ growth of phytoplankton maxima in other lakes and in the oceans (Kiefer et al. 1972; Anderson 1969; Venrick et al. 1973; Kerekes 1974; Juday 1934; Fee 1976) so that the in situ growth theory must also be considered.

Our observations in Lake Michigan indicate that the chlorophyll maximum did not form as a result of a settling out of *Melosira* spp., the dominant forms present during the spring bloom, since the species composition of the newly formed chlorophyll peak did not include large numbers of these species. *Melosira* spp. did sink from the surface waters of the lake following stratification but did not accumulate in the region of the chlorophyll peak. The initial formation of the chlorophyll maximum must, therefore, be attributed to species that appeared as the spring bloom declined and thermal stratification became established.

Following thermal stratification, the species composition within the chlorophyll peak was qualitatively similar to that in the epilimnion, although cells in the peak were several times more abundant than in the epilimion. The similarity in species composition observed at the surface and in the chlorophyll peak supports the hypothesis that sinking contributes to peak development, although the possibility of in situ development is not excluded. More detailed observations during the time of peak formation coupled with production measurements will be required to determine whether the chlorophyll maximum in Lake Michigan is formed by algae growing in the epilimnion and sinking, by cell growth in situ at the depth of the peak, or by a combination of both processes.

Decline of Peak and Autumn Mixing

The collapse of the chlorophyll maxima in 1973 and 1974 occurred in August, in coincidence with storms that upset the physical stability of the system. The depressed thermocline observed on August 27, 1973 and the irregular temperature profile noted on August 13, 1974 (Fig. 1) suggest that storms that occurred on the lake prior to our sampling (U.S. Dep. of Commerce 1973, 1974), and the resulting turbulence and internal waves (Mortimer 1974), contributed to the breakup of the major chlorophyll peak.

Development of the two subsurface chlorophyll peaks in August and September produced a slight increase in integral chlorophyll levels. As autumn mixing commenced and the thermocline descended these peaks were dispersed and incorporated into the epilimnion. This produced a general increase in chlorophyll concentrations in the epilimnion at a time when the total chlorophyll content in the water column was decreasing. Similar increases of surface chlorophyll in Lake Michigan were interpreted by Rousar (1973) as an autumn pulse indicative of eutrophy. The upward mixing of previously formed chlorophyll from the deep peaks accounts for nearly all of the chlorophyll increase observed in the surface waters during September and early October 1973. Samples were not collected at frequent enough intervals to permit a similar analysis in 1974. These observations are similar to those of Fee (1976), who attributed the autumn "bloom" in the Experimental Lakes Area of Ontario not to the upward mixing of nutrients (the classical explanation), but to chlorophyll previously produced in a hypolimnetic peak. Later in the fall as water temperatures decreased and complete mixing was approached in Lake Michigan, the slight increase in chlorophyll that was noted may indeed be new growth in response to increasing nutrient concentrations and a return of winter species to the euphotic zone.

In conclusion, our findings demonstrate the need for adequate resolution in sampling in time and depth, to adequately describe the dynamics of the Great Lakes phytoplankton community. Our description of a subthermocline chlorophyll maximum in Lake Michigan adds a new dimension to studies of phytoplankton, production, and nutrient cycling in

the Great Lakes that must be considered in interpreting the results of previous studies and designing future investigations.

Acknowledgments

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A New Digital Hydroacoustic Data Processor and Some Observations on Herring in Alaska[1]

RICHARD E. THORNE

Fisheries Research Institute, College of Fisheries, University of Washington, Seattle, Wash. 98195, USA

THORNE, R. E. 1977. A new digital hydroacoustic data processor and some observations on herring in Alaska. J. Fish. Res. Board Can. 34: 2288–2294.

A new hydroacoustic data processor using a PDP 11/45 computer was developed and applied to some herring studies in southeastern Alaska. The new processor allows for analysis of up to 50 different depth intervals, has a threshold to eliminate noise, and has greater dynamic range than any previous hydroacoustic data processor. The new system was used to analyze some data previously recorded on analog magnetic tape, including a series of 20 replicate hydroacoustic surveys over a 4-day period in Carroll Inlet. Comparisons were made with an earlier model digital integrator and with results of oscilloscope (CRT) measurements. Results of replicate surveys and comparisons between different areas demonstrated that the distributional characteristics of the herring can greatly affect the results of hydroacoustic surveys.

Key words: hydroacoustic, herring, Alaska, echo integration, digital processor, fish assessment

THORNE, R. E. 1977. A new digital hydroacoustic data processor and some observations on herring in Alaska. J. Fish. Res. Board Can. 34: 2288–2294.

Nous avons mis au point une nouvelle machine de traitement de l'information hydroacoustique à l'aide d'un ordinateur PDP 11/45, et l'avons appliquée à des études sur le hareng dans le sud-est de l'Alaska. Le nouvel organe de traitement permet l'analyse jusqu'à 50 intervalles de profondeur différents, a un seuil d'élimination du bruit et possède une gamme dynamique plus étendue que toute autre machine de traitement précédente. Nous servant du nouveau système, nous avons analysé certaines données enregistrées précédemment sur bande magnétique analogique, y compris une série de 20 relevés hydroacoustiques en double effectuées sur une période de 4 jours dans l'inlet Carroll. Nous comparons avec un modèle plus ancien d'intégrateur numérique et avec des mesures effectuées avec un tube cathodique. Les résultats des relevés en double et les comparaisons entre différentes régions démontrent que les caractéristiques de répartition du hareng peuvent grandement affecter les résultats de relevés hydroacoustiques.

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THE last few years have seen considerable increase in the use of hydroacoustic techniques for fish population assessment because of their powerful sampling capability and potential for real time estimates independent of fishery catch statistics. In particular, principles of echo integration have been applied in several fisheries surveys throughout the world (Thorne 1973a; Johannesson and Losse 1977; Parrish 1975). On the basis of experience with analog echo-integrator systems, a digital-integration system was developed and applied to population studies of Pacific hake (*Merluccius productus*) in 1971 (Thorne 1973b). This system, called DDAPS, was based on a PDP-8L computer. While DDAPS was a considerable improvement over previous analog systems in dynamic range, stability, and versatility, it lacked the power needed for detailed environmental studies or more advanced processing techniques. This paper describes some studies on herring stocks in southeastern Alaska using a larger digital system based on a PDP 11/45 computer. Although the primary incentive for the development of the new system was the extensive processing needs of a coastal upwelling ecosystem study (Thorne et al. 1977), the new processor has considerable potential for fishery resource assessment and has been adapted by the U.S. National Marine Fisheries Service for resource studies in the northeastern Pacific Ocean.

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The Digital Hydroacoustic Data Processor

The new system, as well as DDAPS, was designed to process hydroacoustic data either in real time or from analog magnetic tape from either one or two

echo sounders. The system consists of three major sections: signal-conditioning electronics, analog to digital (A–D) converter section, and the central processor. The signal-conditioning electronics change the signal from the echo sounders into a format suitable for the A–D converter section. The signal is first amplified to match the dynamic range of the processor. The amplified signal is then detected and low-pass filtered. The cutoff frequency of the low-pass filter is selected to correspond to the length of the transmitted pulse of the echo sounder.

The analog to digital converter section consists of an eight-channel multiplex, a 12-bit A–D converter, a programmable clock, two external event inputs, and the computer interface. The section allows sampling of up to eight input signals under program control, at a program selectable rate with an upper limit of 50 kHz.

The central processor is a Digital Equipment Corporation PDP 11/45 with floating point processor, 24 K memory, two 1.2 M word disk drivers, and various input–output devices, including card reader, line printer, and teletypes. The primary program is an echo-integration program written in machine language in which the acoustic signals are squared and integrated in user-selected depth and time intervals, and corresponding fish densities are calculated from input calibration and target strength information. Squaring is accomplished in software rather than in a hardwired multiplier as in DDAPS. The densities are both printed out and stored on disk for further manipulation. Initial input is provided by answering a series of seven questions from the computer as shown in Fig. 1. The duration of the run is set by the number of pings in Question 1, although the run may be terminated at any time by setting a sense switch. Question 2 allows for comment. If all input constant factors in the program are set to unity, the output of the system will be the average squared voltage of the input. The normalizing constant in Question 3 is the factor required to convert this value to fish density and is based on the target strength and acoustic system parameters (source level, gain, and transducer directivity and receiving response). Question 4 provides for a gate-type threshold to eliminate unwanted noise. Question 5 provides the depth intervals and range corrections. Up to 50 continuous intervals may be incorporated, as compared to nine for DDAPS. The range corrections compensate for deviations from the required 20 log $R + 2\alpha R$ depth function. Question 6 provides input for the bottom-tracking routine and is the height above the previous bottom depth where the integration of the signal will terminate. The restriction for the tracking routine is that the bottom depth must not change more than this buffer value between

```
1.  NUMBER OF PINGS ?
 :  600

2.  COMMENT ?
 :   adf bocas de finas - 4 runs

3.  NORMALIZING CONSTANT ?
CHAN 0  :  1

CHAN 1  :  0

4.  THRESHOLD VOLTAGE ?
CHAN 0  :  .07

5.  LIST DEPTHS AND BETA(S)

   D :  50

   D :  60
     B0 :  .714

   D :  70
     B0 :  .833

   D :  80
     B0 :  1

   D :  90
     B0 :  1.25

   D :  100
     B0 :  1.6

   D :  110
     B0 :  2

   D :  120
    B0 :  2.6

   D :  130
     B0 :  3.3

   D :  140
     B0 :  4

   D :  150
     B0 :  4.8

   D :  -1

6.  BOTTOM TRACKING BUFFER ?
 :  9

7.  CURRENT BOTTOM DEPTH ?
 :  159
```

FIG. 1. Example of the input format for the PDP 11/45 hydroacoustic data processor.

successive pings. Information on the position of the bottom signal can be provided by a white-line signal, by a manually positioned signal, or by the bottom signal itself if sufficiently large and discernible from other signals. Question 7 provides the initial position to start the tracking routine.

Example outputs are shown in Fig. 2. Each output includes the number of pings in the run, an information line documenting the time, threshold, and normalizing constant values, and the densities and proportions sampled for each interval. The proportion sampled is <1.0 if the bottom intrudes into the interval.

Major improvements over DDAPS are the greater number of depth intervals, the threshold feature, and greater dynamic range. The PDP 11/45 and A–D converter have a dynamic range of 66 dB, compared with 38 dB for DDAPS. Presently the system is limited by the dynamic range of the signal-conditioning electronics rather than the computer itself. A comparison of input vs. output voltage for the entire system for a 5 kHz input signal is shown in Fig. 3.

Another major advantage is the increased flexibility and versatility possible due to the greater storage and processing power. The echo-integration processing can operate in foreground, while a second program can be run in background. The system will be capable of simultaneous echo-integration and target-strength measurements, and the ability of the computer to access data files stored on disk makes possible further reduction and manipulation of the data using FORTRAN language programs.

Application to Herring Assessment in Southeastern Alaska

Background and Methods

Three series of acoustic surveys on herring in southeastern Alaska were analyzed with the new system as part of its evaluation. The first was a series of 20 replicate surveys over a 4-day period on a large overwintering population of herring in Carroll Inlet, near Ketchikan, Alaska. Ten of these surveys had been previously analyzed by measuring the average amplitude of echoes and the size of the school

```
-1    8.   15:54:23    1.0. 0.100E 01. 0.000E 00. 0.700E-01. 0.000E 00
F =   600                CHAN # 0                    CHAN # 1
  50.0 -   60.0          0.000E 00    1.000
  60.0 -   70.0          0.421E-06    1.000
  70.0 -   80.0          0.169E-05    0.951
  80.0 -   90.0          0.452E-04    0.840
  90.0 -  100.0          0.414E-03    0.744
 100.0 -  110.0          0.460E-03    0.535
 110.0 -  120.0          0.401E-03    0.397
 120.0 -  130.0          0.799E-03    0.350
 130.0 -  140.0          0.420E-03    0.105
 140.0 -  150.0          0.000E 00    0.000

-1    9.   15:59:22    1.0. 0.100E 01. 0.000E 00. 0.700E-01. 0.000E 00
F =   600                CHAN # 0                    CHAN # 1
  50.0 -   60.0          0.521E-06    1.000
  60.0 -   70.0          0.000E 00    0.953
  70.0 -   80.0          0.335E-06    0.839
  80.0 -   90.0          0.248E-04    0.761
  90.0 -  100.0          0.252E-03    0.690
 100.0 -  110.0          0.367E-03    0.660
 110.0 -  120.0          0.295E-03    0.622
 120.0 -  130.0          0.935E-03    0.577
 130.0 -  140.0          0.760E-03    0.493
 140.0 -  150.0          0.105E-02    0.193
```

FIG. 2. Example of outputs from the PDP 11/45 system.

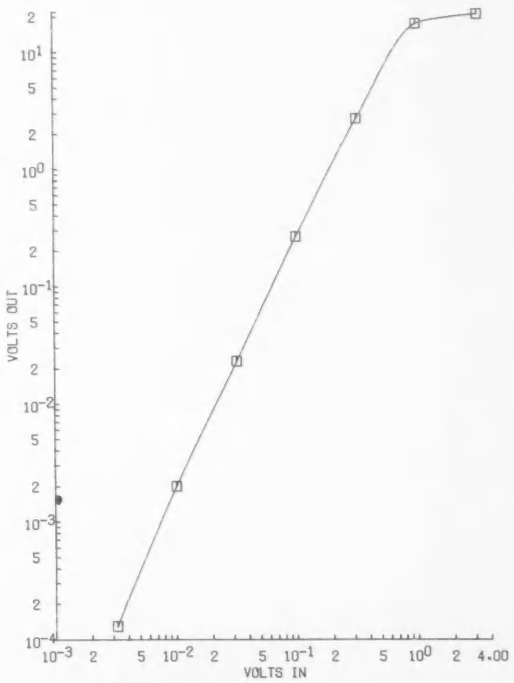

FIG. 3. Relation between input and output voltage for the PDP 11/45 system.

with an oscilloscope (Thorne 1977) and 7 of these 10 had also been analyzed by DDAPS. Thus, the tests with the new processor served to complete the analysis of the series and to compare various methods of analysis.

An additional seven surveys which were run in Carroll Inlet later that winter were also included in the analysis. Five of these had previously been analyzed by oscilloscope (CRT). In addition, four surveys conducted in December 1972 at Bocas de Finas, west of Prince of Wales Island, were reanalyzed. The Bocas de Finas surveys, previously analyzed by CRT, had resulted in the largest population estimates in southeastern Alaska during that year. The herring stock at Bocas de Finas provided an interesting contrast as they were distributed in an extensive layer rather than a school.

All three series had been collected with a data acquisition system which consisted of a 105 kHz Ross 200A Fineline Echosounder modified for collection of data on analog magnetic tape (Thorne et al. 1972). A 7.5° transducer was mounted on the hull of the R.V. *Kittiwake* of the Alaska Department of Fish and Game. Survey procedures usually consisted of defining an area containing the fish school or stock of interest on the basis of previous experience or preliminary search, then running a series of oblique transects spaced evenly over the area.

The new system analyzed 10-m intervals from 10 to 150 m and 5-min duration. Estimates were based on a target-strength assumption of -33 dB/kg, which is presently used for herring surveys in Puget Sound and Alaska with the 105 kHz system and 7.5° transducer. This value

TABLE 1. Results of acoustic surveys in Carroll Inlet.

Date	Run	Starting time	Area (10^3 m^2)	Biomass (10^6 kg)	Comment
Dec. 13, 1972	1	1400	892	1.19	
	2	1419	892	0.54	
	3	1445	892	0.27	
	4	1620	892	0.09	
	5	1731	893	0.48	
	6	1818	1303	0.88	School dividing
	7	1847	995	0.25	
Dec. 14, 1972	8	1755	823	0.05	Missed main body
	9	2139	1475	0.39	2 separate schools
	10	2243	412	0.10	Surveying only 1 school
	11	2304	412	0.05	" " " "
	12	2333	617	0.25	" " " "
Dec. 16, 1972	13	1259	652	0.08	Missed main body
	14	1320	652	0.02	" " "
	15	1425	1406	1.17	
	16	1458	1406	0.44	
	17	1532	1406	1.94	
	18	1605	1441	0.87	
	19	1633	1441	1.05	
	20	1702	1441	0.72	
Feb. 1, 1973	1	1508	1269	0.92	
	2	1553	995	1.91	
	3	1626	514	1.64	
	4	1639	617	1.72	
	5	1749	480	1.18	
Feb. 2, 1973	6	1814	515	0.73	
	7	1844	995	0.22	

was originally determined indirectly by comparisons with net catches in 1972 but has provided reasonable agreement with catch and spawning-ground estimates as well as the initial results with the newly developed dual-beam target strength measuring system (Ehrenberg 1974).

After the basic analysis, the data were further treated by a program which summed the densities over the depth intervals to obtain an average density per unit surface area for each survey. Values were multiplied by the surface areas involved in the surveys to obtain the population estimates.

RESULTS AND DISCUSSION

There was considerable variation among the 27 surveys in Carroll Inlet (Table 1). Some of the variation results from changes in distribution relative to the survey area. Both nights in December, the school divided into at least two parts. Three of the night surveys on December 14 were run on only one of these schools. On at least three other occasions the survey area excluded a significant portion of the population. However, even neglecting these six runs, the standard deviation of the observations was 67% of the mean in December and 52% of the mean in February. The mean in February was about twice as high as in December and probably represents a real increase, as further recruitment into the area is expected in that time period.

Despite the variability among surveys, the comparison between the new system and DDAPS, both referenced to the −33 dB/kg target-strength assumption, was very good (Fig. 4). The mean of the seven runs was 0.57×10^6 kg from the 11/45, 0.54×10^6 kg from DDAPS. The largest component of variability is probably associated with bottom tracking, which was done manually in both cases.

However, the comparison between the 16 estimates from the PDP 11/45 system and corresponding CRT estimates for Carroll Inlet, including estimates from two different readers for seven of the series, was not particularly good (Fig. 5). The CRT method has considerable variability, and biases in reading may even result in nonlinearity. The problems of deriving the population estimate from visually estimated amplitudes is compounded by the fact that the density is related to the squared amplitude (Forbes and Nakken 1972; Ehrenberg and Lytle 1972). Thus, bias is associated with attempting to estimate the average squared amplitude from estimates of the average amplitude, and errors in reading are squared. Results of the comparison confirm our sus-

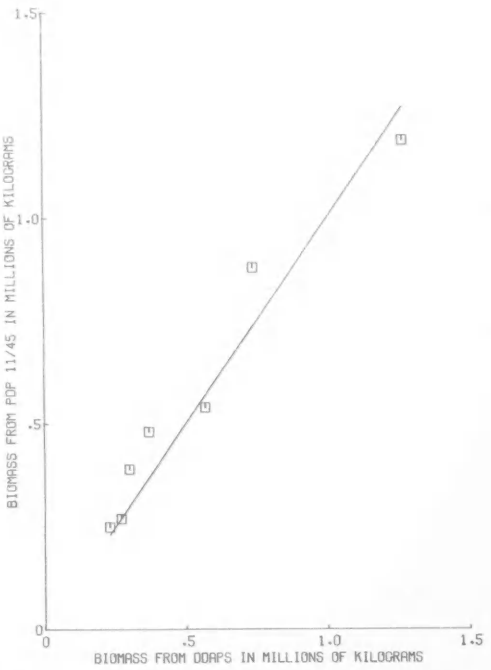

FIG. 4. Comparison between population estimates in Carroll Inlet, December 1972, from DDAPS and PDP 11/45 system.

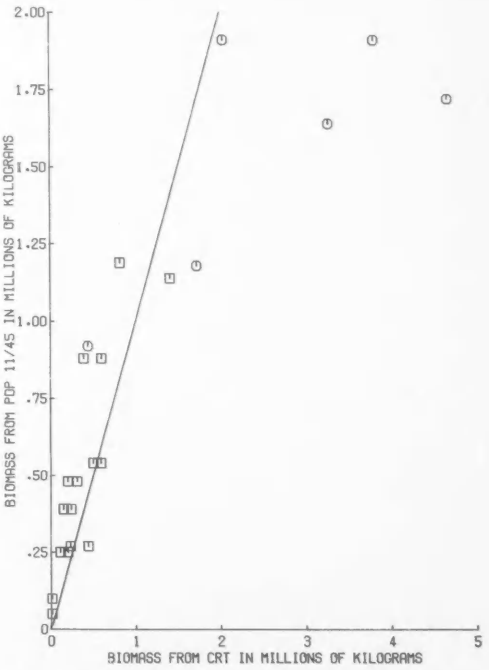

FIG. 5. Comparison between population estimates in Carroll Inlet, December (squares) and February (circles), from CRT and PDP 11/45 system.

picion that the CRT method is not sufficiently accurate, which was the reason for the initial change to DDAPS in 1972.

Agreement among surveys and between 11/45 and CRT estimates was much better for the four runs at Bocas de Finas (Table 2). The standard deviation of the four estimates with the PDP 11/45 was only 17% of the mean and the corresponding CRT estimates were 25% higher with a standard deviation 35% of the mean.

The good agreement among the replicate surveys at Bocas de Finas and also that between the 11/45 and DDAPS at Carroll Inlet clearly show that the major source of variability in the estimates is the distributional characteristics of the fish. At Bocas de Finas the herring are distributed in a layer over an area of about 5 million m^2. In contrast, the school of herring at Carroll Inlet during the day typically occupied about 100,000 m^2.

One of the advantages of the PDP 11/45 system is the capability to process up to 50 different depth intervals simultaneously. This feature allows detailed examination of the vertical distribution of fish. Both the stratification and the diel changes were dramatic for the herring in this study (Fig. 6 and 7). During the day at Carroll Inlet the fish were distributed between 80 and 120 m with a peak at 100 m. At

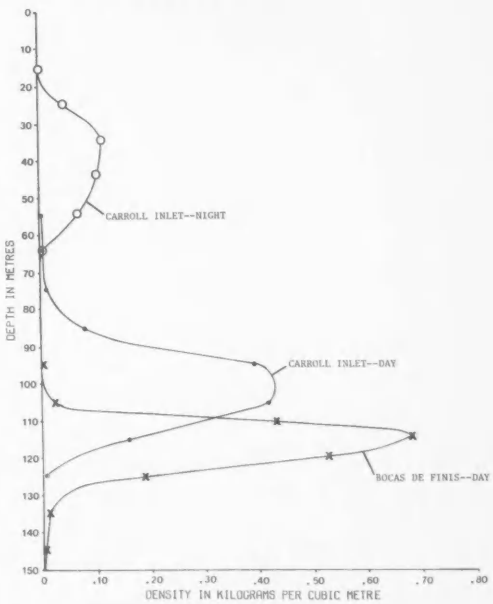

FIG. 6. Vertical density profiles from Carroll Inlet, day and night, and Bocas de Finas during day.

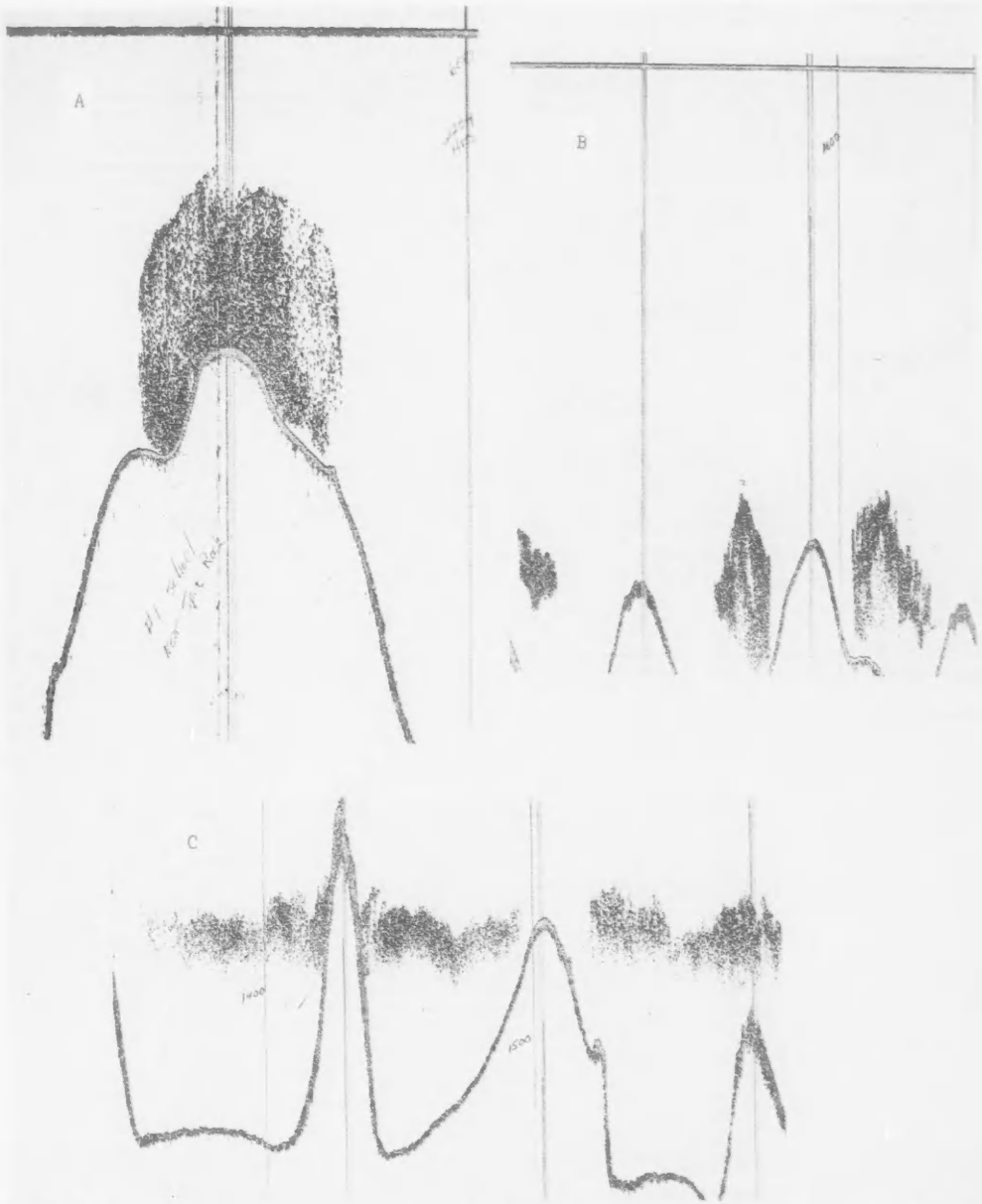

FIG. 7. Echograms from Carroll Inlet, day (A) and night (B) (0–50-fath scale), and Bocas de Finas during day (C) (50–100-fath scale).

night, peak abundance was about 40 m, densities were lower, and horizontal extent was greater. The echogram (Fig. 7) also shows a strong shoreward bias at night at Carroll Inlet. The lower estimates at night could be the result of distribution too near shore to be included in the boundaries of the survey. The depth stratification was even more pronounced at Bocas de Finas, with a depth of maximum density at about 115 m. The more uniform horizontal distribution is readily seen from the echogram.

TABLE 2. Results of acoustic surveys in Bocas de Finas.

Date	Run	Start time	Area (10^6 m^2)	Biomass (10^6 kg)	Original CRT estimate (10^6 kg)
Dec. 2 1972	1	1232	8.3	8.0	7.1
	2	1425	8.3	11.7	16.5
Dec. 3 1972	3	1215	7.2	10.9	15.2
	4	1308	7.2	8.8	10.6

Conclusions

The most apparent advantage of the PDP 11/45 system over DDAPS in this study was the ability to access the data files on disk for rapid data reduction. The greater dynamic range is less important for tape-recorded data, since optimal amplification can be set from a knowledge of the recorded levels, and even DDAPS is as good as most analog recorders in dynamic range. Similarly, the detailed information on vertical distributions and diel variations is very interesting from behavioral and ecological aspects, but unimportant for total stock assessment of a single species population. Nevertheless, the capability of the system is clearly demonstrated even for the specific requirements of herring stock assessment. There are presently six acoustic systems that collect data on herring in Washington and Alaska, often with requirements for data analysis within 24 h, so the greater storage and processing capability is a significant advantage.

Analog data recording is practical for the herring surveys which are of typically short duration on inside waters. The advantages of the PDP 11/45 system are more apparent when one considers the complex processing requirements of major offshore resource assessment surveys. Simultaneous echo-integration and target-strength measurement are virtually a necessity in the typical multispecies marine environment. The capability for additional programs, such as readily incorporating trawl data or even historical records, to partition abundance by species, provides a processing ability previously unavailable in resource assessment research.

Acknowledgments

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The surveys in southeastern Alaska were conducted and supported by the State of Alaska Department of Fish and Game (ADF&G). Special thanks are due the ADF&G biologists who aided in the data collection, especially S. Moberly, the herring project leader, and also to the crew of the R.V. *Kittiwake*.

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Investigation of the Impact of Mercury on Enclosed Water Columns Using a Zooplankton Simulation Model

NICHOLAS C. SONNTAG

Institute of Oceanography, University of British Columbia, Vancouver, B.C. V6T 1W5

AND WULF GREVE

Biologische Anstalt Helgoland (Meeresstation), 2192 Helgoland, Federal Republic of Germany

SONNTAG, N. C., AND W. GREVE. 1977. Investigation of the impact of mercury on enclosed water columns using a zooplankton simulation model. J. Fish. Res. Board Can. 34: 2295–2307.

A computer simulation model of a phytoplankton–zooplankton–salmon system is used to investigate possible causes of different *Pseudocalanus minutus* s.l. population dynamics in three enclosed water columns. Mercury at 1 and 5 $\mu g/\ell$ was added to two enclosures, with the third serving as a control. Represented in the model are diatoms, flagellates, *P. minutus*, and fingerling chum salmon (*Oncorhynchus keta*). Population dynamics are represented in terms of age structure, with age-dependent feeding and survival. Real world data are used to represent the phytoplankton densities. The model results support a hypothesis that the observed *Pseudocalanus* populations after day 25 could have been a direct consequence of different flagellate populations in the enclosures rather than lethal effects of mercury on molting and reproduction success of the copepod.

Key words: modeling, simulation, controlled ecosystems, mercury, zooplankton dynamics

SONNTAG, N. C., AND W. GREVE. 1977. Investigation of the impact of mercury on enclosed water columns using a zooplankton simulation model. J. Fish. Res. Board Can. 34: 2295–2307.

Nous avons utilié un modèle simulé sur ordinateur d'un système phytoplancton–zooplancton–saumon pour déterminer les causes possibles de différences observées dans la dynamique de populations de *Pseudocalanus minutus* s.l. dans trois colonnes d'eau fermées. Nous avons ajouté du mercure à des concentrations de 1 et de 5 μg/litre à deux colonnes, alors que la troisième servi de témoin. Des diatomées, des flagellés, *P. minutus* et des fingerlings de saumon keta (*Oncorhynchus keta*) apparaissent dans le modèle. La répartition des âges, avec une alimentation et une survie dépendant de l'âge, sert à représenter la dynamique des populations. Des données cueillies sur le terrain ont été utilisées pour indiquer les densités de phytoplancton. Les résultats du modèle corroborent l'hypothèse que les populations de *Pseudocalanus* observées après 25 jours ont pu être une conséquence directe des différentes populations de flagellés dans les colonnes d'eau plutôt que des effets létaux du mercure sur le succès de la mue et de la reproduction du copépode.

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AN introduction to the Controlled Ecosystem Pollution Experiment (CEPEX) program and the specifics of the 1976 mercury experiment are presented in Grice et al. (1977). Essentially, three 1300-m^3 close-ended bags (Controlled Experimental Ecosystems, CEEs) made of transparent polyethylene were filled simultaneously in Saanich Inlet, B.C., by being raised to the surface from 35 m in late May 1976. The bag diameter was 10 m and depth was approximately 23 m. Each bag initially contained approximately equal amounts of phytoplankton and zooplankton. One bag served as the control (CEE C). The others were polluted on day 8 with mercury, one to 1 $\mu g/\ell$ (CEE 1) and the other to 5 $\mu g/\ell$ (CEE 5). On day 10, 55 fingerling chum salmon (*Oncorhynchus keta*) were added to each enclosure. The only other perturbations imposed on the bags were the removal of 10 salmon on day 16 and a further 8 on day 44, and the addition of nutrients on days 25, 37, and 53. The nutrient addition on day 25 consisted of sediments pumped from the bag bottom only, while the additions on days 37 and 53 consisted of bottom sediments and commercially available inorganic nutrients. The dynamics of the three enclosures were monitored for 70 days.

The observed phytoplankton averaged over 0–12 m and "total" copepod populations are shown in Fig. 1 and 2. Copepods represented the primary component of the "total" zooplankton with the

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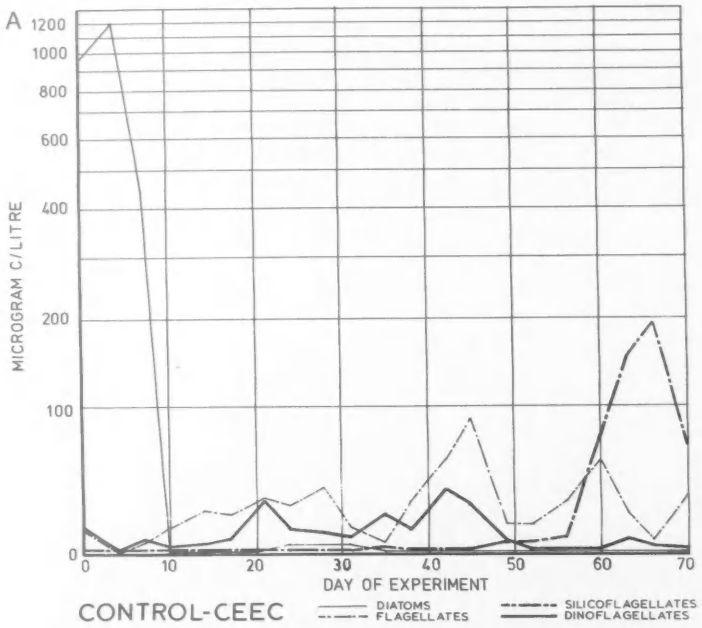

FIG. 1A. Observed biomass of the major phytoplankton groups. CEE C (Thomas et al. 1977b).

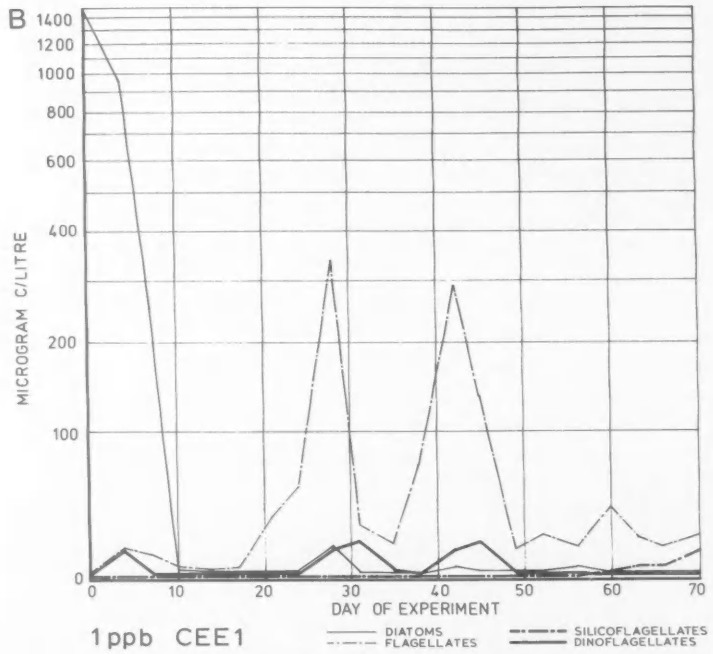

FIG. 1B. Observed biomass of the major phytoplankton groups. CEE 1 (Thomas et al. 1977b).

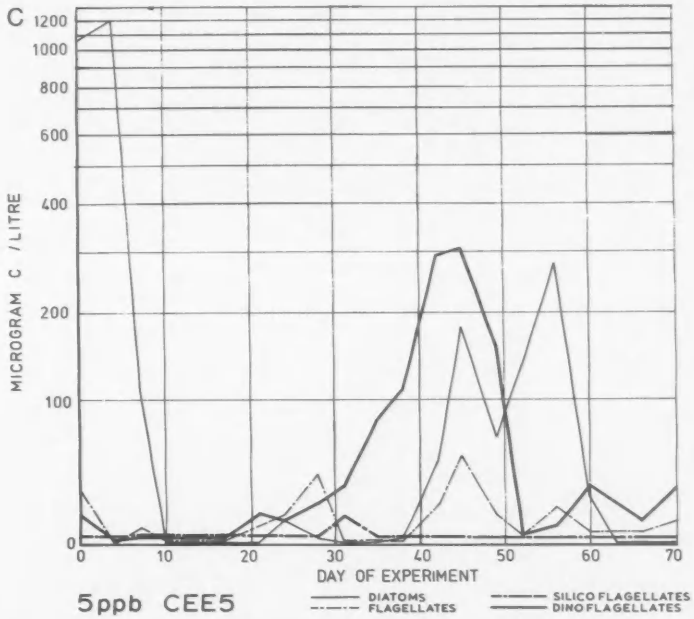

FIG. 1C. Observed biomass of the major phytoplankton groups. CEE 5 (Thomas et al. 1977b).

dominant forms in each enclosure being *Pseudocalanus, Acartia, Centropages, Paracalanus*, and *Calanus*. These abundances were derived from analysis of pump collections and bongo net tows from four vertical profiles in each CEE: three replicates in the top 16 m and one in the bottom 7.5 m. For the purposes of this paper the key points to notice are:

1) The total copepod population in CEE 5 was dramatically lower than in CEE C and CEE 1, especially in the latter half of the experiment.

2) The four dominant phytoplankton groups in each CEE are different after day 24. Of special interest is the presence of two microflagellate blooms in CEE 1 and the dinoflagellate bloom in CEE 5.

In this paper we follow the precedent set by Grice et al. (1977) and are considering only the dominant copepod *Pseudocalanus minutus*. In CEE 5 no ovigerous female *Pseudocalanus* were seen between days 11 and 25. Adult females isolated on day 15 did not produce eggs over a 7-day period and stage V females maintained in CEE 5 water failed to molt when fed a standard phytoplankton ration (Grice et al. 1977). As a consequence, Grice et al. (1977) and Beers et al. (1977) claim that the lower CEE 5 zooplankton populations in the latter part of the experiment are a direct impact of these observed effects of mercury on copepod molting success and fecundity. However, since from day 24 on the phytoplankton populations are significantly different in each bag, it seems reasonable to hypothesize that the herbivores would develop differently irrespective of any continued effects on zooplankton physiology.

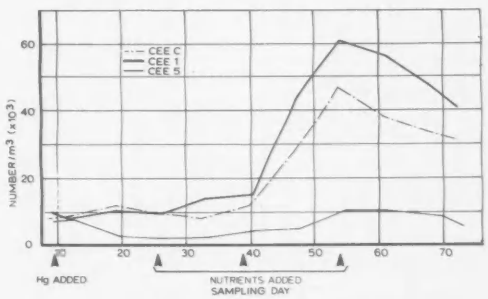

FIG. 2. Observed total copepod populations in each bag (Grice et al. 1977).

Figure 3 shows the possible interactions generating the *Pseudocalanus* population in CEE 5. The problem is to determine which interactions directly determine the *Pseudocalanus* population. We attempt to do this using a computer simulation model. The key issue is whether the different *Pseudocalanus* populations after day 24 were a direct consequence of (1) the impact of mercury on the *Pseudocalanus* physiology, or (2) the phytoplankton population available as food. Keeping that objective

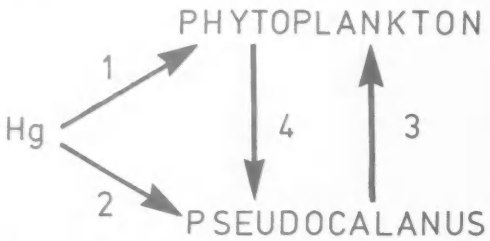

FIG. 3. Major interactions influencing zooplankton development in a mercury polluted bag.

in mind we did not attempt to model primary production, thereby eliminating interactions 1 and 3 in Fig. 3. Instead we use the determined phytoplankton carbon as input data to drive a zooplankton model. We do not claim that interactions 1 and 3 don't exist; we need to know only that the phytoplankton populations are different, not why. Therefore, the simulation will be used for a specific narrow test to see if the different phytoplankton populations after day 24 are sufficient to generate the observed *Pseudocalanus* dynamics or whether it is necessary to invoke the physiological effects of mercury on the CEE 5 *Pseudocalanus* after day 24.

The Zooplankton Model

General Description

Over the last 20 yr marine plankton ecosystems have formed the basis for many theoretical studies, mainly in terms of biomass (e.g. Riley et al. 1949; Steele 1958; Winter et al. 1975) but also with some separation of a herbivore species into size or age-classes (e.g. Steele 1974; Steele and Henderson 1976). More recently Steele and Frost (1977) have identified a need in models for more explicit recognition of a trophic level's species composition and population dynamics.

The model presented here incorporates the population structure of the filter feeding copepod *Pseudocalanus* and young chum salmon. Other carnivores (i.e. ctenophores, etc.) did not appear in the bags and were therefore excluded from the model. The model is a collection of simple component descriptions linked together over time to facilitate investigation of the dynamics of the system's populations as a function of the interactions shown in Fig. 4. Since the physical structure of the CEPEX bags represents an isolated ecosystem, the emphasis can be placed on the biological interactions and the impact of the physical components such as advection and turbulence can be essentially ignored.

The variables driving the model are the experimentally determined phytoplankton densities taken at intervals of 3 or 4 days over a period of 70 days. The main state variables are:

a) *Pseudocalanus* age-class densities (number/m^3);

b) salmon biomass (g C/m^3);

c) nutritional status of (a) and (b).

It is important to note here that the model expresses change in density, expressed as numbers or biomass per cubic metre, and therefore represents a completely mixed (homogeneous) bag with no spatial components.

The rules of change in the model are essentially a function of each age-class population's predation success and a natural mortality function. The model does not account for any of the aspects of primary production (nutrients, sinking, etc.), nor does grazing affect the composition or biomass of the phytoplankton.

The key parameters in the model are:

a) a maximum birth factor for *Pseudocalanus* (nauplii 1/female) and a maximum salmon growth factor (% body weight/day);

b) predation interaction factors expressing an efficiency of encounter for the respective predator and prey;

c) the natural mortality expressed as a fraction of the population per day; and

d) the maximum mass of carbon that can be assimilated by each age-class per day.

The model, programmed in FORTRAN, is operated via a simulation control language, SIMCON (Hilborn 1973), available on the UBC IBM 370/168 system.

To simulate the change over time for each of the variables the computer program takes the value of each index at the start of a simulated day, and finds a new value for it at the start of the next day. These calculations (or rules of change) are applied repeatedly for 70 days. The sequence of calculation within any simulated day is shown in Fig. 5.

The model uses CEPEX site data to provide (1) starting estimates of *Pseudocalanus* and salmon populations; and (2) the daily phytoplankton densities available to *Pseudocalanus*.

The following sections give detailed descriptions of the main calculations that are made each day in a simulation sequence. Assumptions used in the calculations are made clear whenever possible.

The Phytoplankton Population

For the purpose of the model the phytoplankton populations (Fig. 1) are aggregated into two groups. The larger particles (diameter greater than 10 μm), collectively called diatoms, are the sum of diatoms, dinoflagellates, and silicoflagellates. The smaller particles, to be called flagellates, are the microflagellates. These time series, expressed as μg C/m^3, are used to drive the model. Since the model operates on a daily basis, a linear interpolation is executed between data points. This assumes there are no smaller

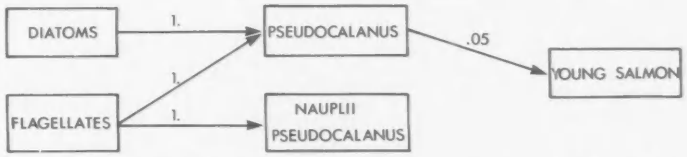

FIG. 4. Flow chart of simulation model. Each arrow represents the direction of energy flow in a predator–prey interaction contained in the model. Numbers beside each arrow are the interaction efficiency coefficients described in the text.

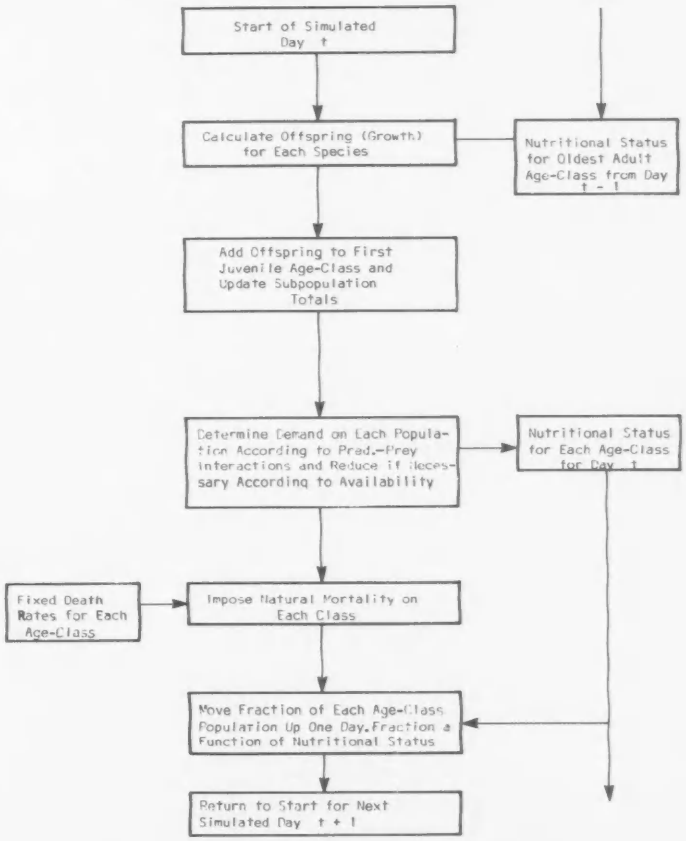
Start of Simulated Day t
Calculate Offspring (Growth) for Each Species
Nutritional Status for Oldest Adult Age-Class from Day t - 1
Add Offspring to First Juvenile Age-Class and Update Subpopulation Totals
Determine Demand on Each Population According to Pred.-Prey Interactions and Reduce if Necessary According to Availability
Nutritional Status for Each Age-Class for Day t
Fixed Death Rates for Each Age-Class
Impose Natural Mortality on Each Class
Move Fraction of Each Age-Class Population Up One Day, Fraction a Function of Nutritional Status
Return to Start for Next Simulated Day t + 1

FIG. 5. Sequence of calculation in a simulated day.

time-scale phenomena causing large fluctuations between the data points.

ZOOPLANKTON FEEDING

The *Pseudocalanus* population is divided into age-classes where the number of age-classes equals the average number of days, N, for a healthy organism to mature from egg to adult. The first $N/2$ age-classes represent the *Pseudocalanus* nauplii population and the remaining $N/2$ age-classes represent the *Pseudocalanus* copepodite population (Table 1). The term "total *Pseudocalanus*" will refer to the sum of the last $N/2$ age-classes (i.e. copepodite I [CI] to adult). The last copepodite age-class is called the adult age-class. Members of the adult age-class are removed either through natural mortality or predation (see below). The age-classes should not be thought of as weight-classes although there is obviously an implicit

TABLE 1. Some model parameters used in standard run.

	Pseudocalanus
No. of age-classes, N	30[a]
Maximum nauplii I/female adult	4/day[b]
Max. assimilation nauplii VI	.2 μg C/day[c]
copepodite (adult)	3.25 μg C/day[d]

[a]Paffenhofer and Harris (1976).

[b]Paffenhofer and Harris (1976): Rather than simulate egg production directly we represent reproduction as the average number of nauplii I generated per adult female. The 1- or 2-day delay in the egg stage is implicitly accounted for in the 30-day age-class structure.

[c]To calculate this parameter it was assumed that the maximum μg C ingested/μg C animal for adult *Pseudocalanus* was the same for N VI *Pseudocalanus*. For subarctic copepods carbon wt/dry wt ≃ .5 (Parsons and Takahashi 1973); adult wt ≃ 20 μg dry wt; N VI wt ≃ 1.4 μg dry wt (Paffenhofer and Harris 1976); therefore, max. assimilation N VI = (3.25/(20*.5))* (1.4*.5) ≃ .2 μg C/day.

[d]Combination of figures 3 and 4 in Frost (1974).

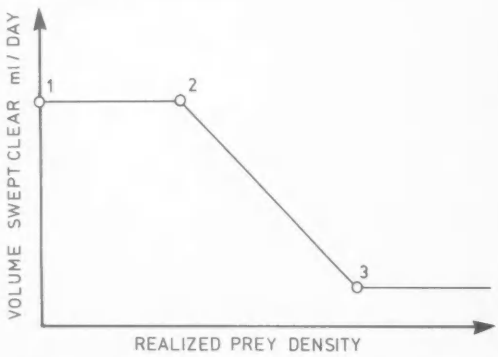

FIG. 6. General shape of filtration rate curve used in model. Points 1, 2, and 3 are the critical points mentioned in the text and summarized in Table 2.

weight associated with each class. The purpose of the age-classes is to provide a simple and rational mechanism to represent the time lag between egg production and the emergence of adults.

In the model the zooplankton are assumed filter feeders only and a grazing rate is determined for each age-class. The filtration rate curves are all of the shape shown in Fig. 6. The coordinates of the three critical points indicated are required for the oldest and youngest naupiii and copepodite age-classes (Table 2). For the age-classes between the extremes these points are determined by linear interpolation. Since the exponents in Fig. 3 of Paffenhofer and Harris (1976) fluctuate around 1.0 for *Pseudocalanus elongatus*, a linear approximation appears adequate at present.

TABLE 2. Critical points for filtration rate curve in Fig. 6. For *Pseudocalanus* (x, y) = (μg C/m³, ml/day). For salmon (x, y) = (no. *Pseudocalanus*/m³, m³/day).

	Pseudocalanus[a]		
	Nauplii	Copepodite	Salmon[b]
Point 1			
Maximum	(0, 2)	(0, 40)	(0, 5)
Minimum	(0, .5)	(0, 3)	—
Point 2			
Maximum	(7×10^4, 2)	(8×10^4, 40)	(10^4, 1)
Minimum	(6×10^4, .5)	(7×10^4, 3)	—
Point 3			
Maximum	(3×10^6, .05)	(3×10^6, 1)	(10^5, .1)
Minimum	(3×10^6, .01)	(3×10^6, .1)	—

[a]Maximum filtration rate for adult *Pseudocalanus* was calculated from figure 4, Frost (1974). To calculate remainder the ratios (f. rate adult/f. rate N VI) were calculated for *Calanus pacificus* from Frost (1972), and Mullin and Brooks (1970) and it was assumed ratios would be the same for *Pseudocalanus minutus*.

[b]A. Newall, U.B.C., Vancouver, personal communication.

For the *Pseudocalanus* total nauplii and total copepodites, a "realized" μg C/m³ density of phytoplankton is used as the "prey" concentration for each age-class comprising the total. By "realized" is meant that if a copepod has a feeding efficiency of 10% for flagellates then the μg C/m³ (i.e. prey density) to which it will react (i.e. determine a filtration rate according to Fig. 6) is 10% of the actual flagellate concentration in the water. This is done (a) to ensure that the zooplankton feeding is is a reaction to potential ingested carbon; and (b) to account for the observed particle size selectivity of grazing zooplankton (Parsons and LeBrasseur 1970). The feeding efficiencies for all interactions are shown in Fig. 4. Having determined the realized prey densities for the total nauplii and total copepodite groups, the daily filtration rates for each individual age-class are calculated and applied to the appropriate interactions to determine the total system demand upon each population. Each age-class within a nauplii or copepodite total sees the same "realized" prey density but has different filtration rate reactions according to their age-class.

SALMON FEEDING

Salmon have a "realized" prey density measured in terms of numbers of *Pseudocalanus* rather than micrograms C. The salmon feeding behavior is modeled as a volume searched per day with a success of

encounter parameter for *Pseudocalanus*; the number of encounters equals the volume searched times the density of prey. The simplicity of this approach is meant to simulate the qualitative rather than quantitative aspects of salmon growth.

Natural Mortality

From the literature one concludes that there are other factors contributing to a maturing copepod's probability of survival besides predation (Corkett 1967; Paffenhofer and Harris 1976). This is reinforced by this mercury experiment in which *Pseudocalanus* cohorts in CEE C and CEE 1 experienced large reductions in population from egg to adult despite the lack of any significant carnivore population (Beers et al. 1977). We have chosen to call this mortality factor, "natural mortality."

Examples of mechanisms that we would include in "natural mortality" are:

1) repeated starvation of individual *Pseudocalanus* due to the patchy food environment in the unmixed bags;

2) varying probabilities of survival due to physiological differences affecting a copepod's resilience to natural perturbations;

3) carnivore predation and cannibalism within the copepod community (Corner et al. 1976).

Rather than include these explicitly in the model and thereby, we feel, unnecessarily increase its complexity we have chosen to accumulate all these factors into the component "natural mortality." To represent "natural mortality" in the model we have used a relation suggested by Cushing (1976) for the pelagic community $N_t = N_o/1 + \alpha t$ where t = number of days, N_o = number of organisms at $t = 0$, N_t = number of organisms at $t = t$, α = parameter determing degree of convexity of the curve.

This formulation results in a high mortality over the first few days of a zooplankter's life and drops off monotonically to relatively low rates for older animals. Using this expression the model determines the equivalent percent mortality for each age-class and removes the appropriate amount each day.

The net nauplii I to adult *Pseudocalanus* "natural mortality" recorded in the literature ranges from 70% (Corkett 1967) to as low as 30% (Paffenhofer and Harris 1976). Since these are in laboratory conditions, presumably more favorable to a copepod's survival, we feel justified in taking a net "natural mortality" of 80%. This would imply $\alpha = .12$ for a *Pseudocalanus* that matures from nauplii I to adult in 30 days.

Population Dynamics

To advance each age-class population the assimilated carbon (80% assimilation efficiency) of an individual organism in the age-class is compared to a predetermined maximum (Table 1).[1] If the carbon assimilated exceeds this maximum, that age-class population is moved up 1 day and any excess ingestion is assumed superfluous feeding. On the other hand, if the assimilated carbon is less than the maximum then only a proportional amount of the age-class population is advanced, the remainder stays (i.e. proportion = carbon assimilated per maximum; this fraction is defined as the zooplankton's nutritional status).

For the nauplii age-classes the implications of low food availability (i.e. low nutritional status) can be quite dramatic because of the high natural mortalities being applied repeatedly to the same populations.

Reproduction is calculated at the beginning of a simulated day. It is assumed that only the members of the adult age-class reproduce and that 50% of them are female (Table 1); the maximum possible number of nauplii I is determined and then reduced according to the adult age-class' nutritional status. They are then added into the population of the first age-class.

For salmon a simple growth model is used based on the data of Parsons and LeBrasseur (1970). The maximum daily assimilation possible for salmon is assumed to be 10% of their biomass expressed in grams C. Their maximum growth rate is 5% per day, which is reduced according to the salmon's nutritional status, determined in the same manner as for *Pseudocalanus*.

Results

The starting conditions for the *Pseudocalanus* and salmon populations are given in Table 3. As indicated, groupings of the model age-classes are assumed equal to nauplii and copepodite stages. The nauplii data available at the time of writing were a total number for all copepod species. For the purposes of the model it was assumed that total *Pseudocalanus*/total copepodites = total *Pseudocalanus* nauplii/total copepod nauplii. The resulting totals were distributed evenly between the nauplii age-classes.

For salmon the equivalent biomass of 45 chum fingerlings (the number after day 15) is introduced into the model on day 15 (see Grice et al. 1977). To simulate the removal of 8 fish from each bag on day

[1]The maximum corresponds to the ingestion rate at which the filter feeder is satiated. For higher prey densities it will lower its filtration rate to maintain constant ingestion. Since the filtration rates used here have a linear decline after satiation, they will over-harvest what the copepod actually needs for constant ingestion. Each age-class has its own maximum assimilation determined by linear interpolation between the specified maximums for the nauplii and copepodite stages.

TABLE 3. Starting conditions for *Pseudocalanus* and salmon. For *Pseudocalanus* the numbers are the initial population of each model age-class (number/m^3). Salmon is represented as an equivalent biomass/m^3 (i.e. 45 fish * g C of 1 fish/volume of bag).

Stage	Model age-classes	CEE 1	CEE 5	CEE C
Nauplii (I–VI)	1–15	1812	486	1140
Cop. I	16–18	804	645	745
Cop. II	19–21	671	516	660
Cop. III	22–24	460	307	218
Cop. IV	25–27	197	120	130
Cop. V	28–29	320	240	383
Adult	30	895	294	767
Salmon		.0026 g C/m^3	.0026 g C/m^3	.0026 g C/m^3

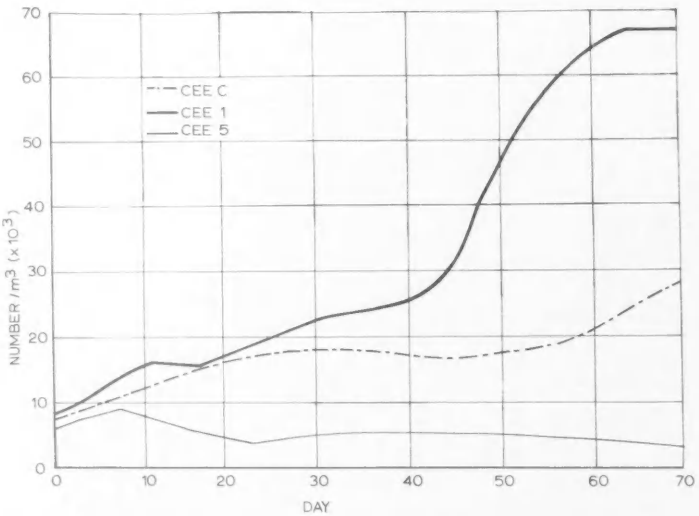

FIG. 7. Simulated total *Pseudocalanus* (CI to adult) populations (standard run).

44, 18% of the salmon biomass is removed at that time.

The model-generated *Pseudocalanus* populations for CEE 1, CEE 5, and CEE C are presented in Fig. 7. For all three model experiments the rules of change were as described in the previous section. The only changes in the parameters were for CEE 5. To simulate the physiological changes in molting success and fecundity discussed earlier the birth factor for *Pseudocalanus* was set to zero and the population was prevented from advancing through the age-classes between days 8 and 24. After day 24 all the parameters were returned to normal. Comparing the curves with the experimental data in Fig. 8 we see that the model replicates the observed behavior surprisingly well. The total *Pseudocalanus* (CI-adult) populations in CEE 1 and CEE C reach their maximum in the latter half of the model run, while in CEE 5 the total *Pseudocalanus* never exceeds 10,000/m^3. What is important to notice here is that the model demonstrates the dramatic qualitative difference in behavior of *Pseudocalanus* for CEE 1 and CEE 5 without any of the reported CEE 5 changes in reproduction or molting success after day 24. In the context of the model this difference results from the very different flagellate populations in the two bags between day 21 and day 50, especially the two peaks on days 28 and 42 in CEE 1 (see Fig. 1). Total *Pseudocalanus* populations have 100% feeding efficiency on both flagellates and diatoms (Fig. 4). However, the *Pseudocalanus* nauplii feed only on flagellates. Consequently, the lack of flagellate carbon in CEE 5 results in a low nutritional status for *Pseudocalanus* nauplii causing a retardation in their movement through the age-classes. Thus, as a consequence of natural mortality few of the nauplii survive to the copepodite stage. This is illustrated in Fig. 9, summarizing the simulated *Pseudocalanus*

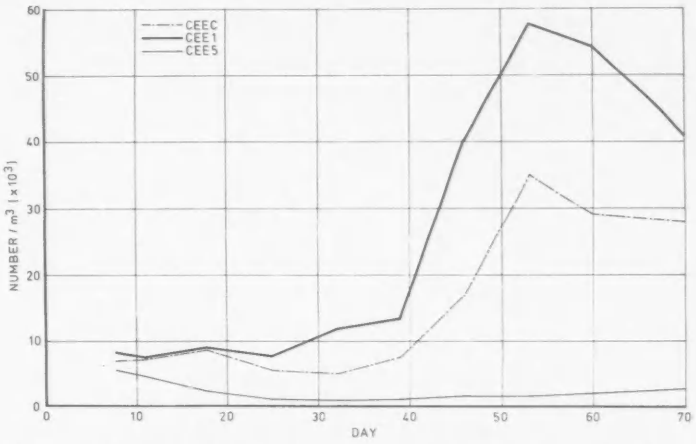

FIG. 8. Observed total *Pseudocalanus* (CI to adult) population (Grice et al. 1977).

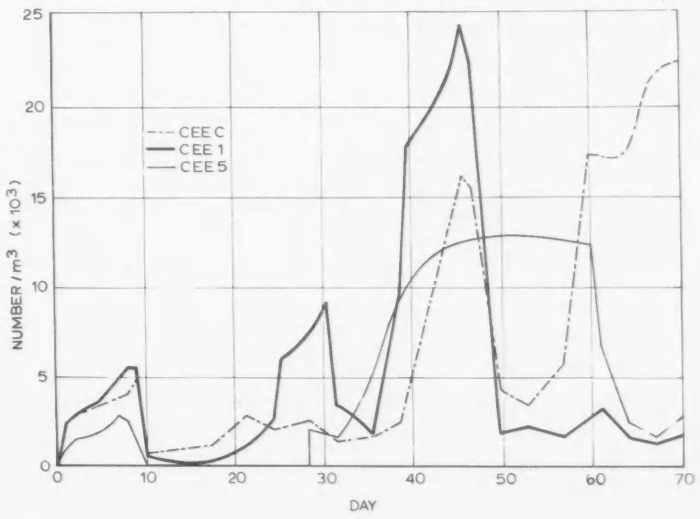

FIG. 9. Simulated population of first *Pseudocalanus* nauplii age-class (standard run).

nauplii I production and Fig. 10, showing the simulated number of nauplii VI which age to copepodite I each day. The CEE 1 nauplii I production peak on day 31 in Fig. 9, resulting from the adults feeding well on the first flagellate bloom, is successfully transmitted through the nauplii stages into the copepodite stage (Fig. 10) by the second flagellate bloom on day 42. This is reflected by the sudden rise of total *Pseudocalanus* in Fig. 7 on day 42.

On the other hand, although the CEE 5 simulated *Pseudocalanus* nauplii I production compared to that of CEE 1 is of a reasonable level over days 35–60, few nauplii survive to reach the copepodite stage (Fig. 10) due to the lack of flagellate carbon.

The experimental data for *Pseudocalanus* egg populations corroborate the above causal mechanism for CEE 1. Beers et al. (1977) report total numbers of eggs reaching maximum values of 41,000/m³ and 97,000/m³ on days 39 and 50, respectively, and saw a significant population of eggs on day 31 (approximately 26,000/m³). They also report a very high nauplii mortality (71%) for the CEE 1 cohort generated on day 50 which was also seen to occur in the model (Fig. 9 and 10). Unfortunately, no

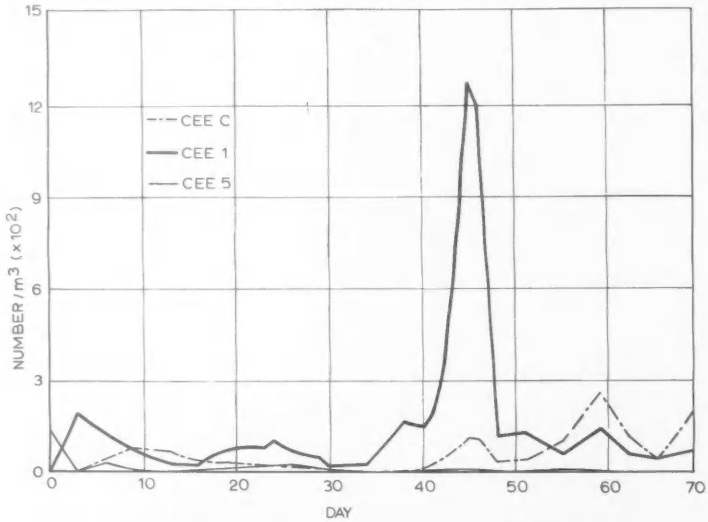

FIG. 10. Simulated number of *Pseudocalanus* nauplii successfully molting to the first *Pseudocalanus* copepodite age-class (standard run).

egg or nauplii data are available for CEE 5 or CEE C so further comparisons between the model and the experimental populations are not possible.

To investigate the model's sensitivity to natural mortality we lowered first the α parameter in equation 1 and second the required μg C assimilated/day for each *Pseudocalanus* nauplii age-class. Model experiments were done for $\alpha = .05$ and $\alpha = .01$, resulting in egg to adult net natural mortalities of 60 and 23%, respectively. Similarly, model experiments were done for maximum micrograms C assimilation for *Pseudocalanus* nauplii of .1 μg C/day and .05 μg C/day. The results are shown in Table 4. The shapes of the curves were similar to those in Fig. 7. Although the population numbers change, the qualitative differences between the two bags are preserved. This implies that natural mortality, although a key determinant in the maximum number reached, is not controlling the qualitative differences in model behavior.

The predicted *Pseudocalanus* population for CEE 5 is sensitive to the assumption that *Pseudocalanus* nauplii cannot feed on the model diatom population. The model diatom population for CEE 5 is made up of two groups, the chain forming diatom *Chaetoceros* spp. and the dinoflagellate *Gymnodinium* spp. (15 μm and 25 μm) (later reidentified as *Scrippsiella trochoideum* (15 μm)) (Thomas et al. 1977b). Hargrave and Geen (1970) found that nauplii of *P. minutus* could not survive on *Chaetoceros* sp. and in fact concluded that they could not feed very successfully on cells > 5 μm in diameter. To the author's knowledge, the only other investigation encompassing the feeding characteristics of *Pseudocalanus* nauplii is the recent work by Paffenhofer and Harris (1976). They were able to raise *P. elongatus* from egg to adult on the diatom *Thalassiosira rotula* (cells of 20–22 μm in chains of up to 16 cells). However, the primary purpose of their work was to measure the growth characteristics and fecundity of *P. elongatus* and not its feeding selectivity. Consequently, to ensure that their animals had adequate food they agitated the *T. rotula* in a "supermixer" prior to use to reduce the chain length. This, we feel, makes any conclusion that *Pseudocalanus* nauplii can survive on cells larger than 5 μm highly tenuous. There is no guarantee that the mixing didn't break up some of the individual cells into particles more easily ingested by the nauplii.

TABLE 4. Results of sensitivity tests on changes in the natural mortality parameter, α, and in maximum micrograms C ingested for *Pseudocalanus* nauplii VI. Entries are the maximum total *Pseudocalanus* (CI to adult)/m³ reached in a 70-day simulation. The day on which the maximum occurred is enclosed in parentheses.

	Mortality parameter Standard $\alpha = .12$		Maximum ingestion Standard = .2 μg C/day	
	$\alpha = .05$	$\alpha = .01$	.1 μg C/day	.05 μg C/day
CEE 1	83,600 (day 70)	151,000 (day 70)	72,000 (day 63)	91,800 (day 63)
CEE 5	14,300 (day 54)	41,900 (day 70)	10,800 (day 54)	30,400 (day 70)

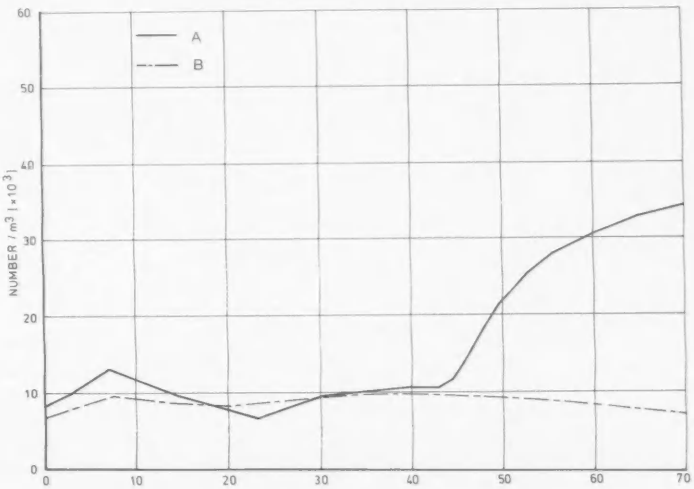

FIG. 11. Simulated total *Pseudocalanus* population (CI to adult) for: (A) CEE 1 phytoplankton population and initial conditions but with reported CEE 5 drop in copepod fecundity and molting success imposed between days 8 and 24; (B) CEE 5 phytoplankton population and initial conditions but with no drop in copepod fecundity and molting success between days 8 and 24.

As for the *Scrippsiella* sp., some feeding experiments will be carried out with *Pseudocalanus* nauplii in the near future. In the meantime we feel justified in claiming a "zero" feeding efficiency between *Pseudocalanus* nauplii and the large particle population, "diatoms."

To demonstrate the robustness of the model's predictions, two simulations were run (Fig. 11). The first is a simulation of CEE 5 without the drop in fecundity and molting success between days 8 and 24. The second is of CEE 1 with the drop in fecundity and molting success imposed between days 8 and 24. Note that the qualitative difference between the two bags is preserved. From this we conclude that in the context of the model the reported impacts of mercury on *Pseudocalanus* physiology are not on their own sufficient to generate the observed differences in the *Pseudocalanus* populations.

For salmon the model-predicted biomass (g C/m³) is summarized in Fig. 12. Despite the low feeding efficiency assumed for the salmon–*Pseudocalanus* interaction (5%), the salmon in CEE 1 and CEE C did significantly better than those in CEE 5, replicating favorably the observed salmon behavior (Grice et al. 1977). This is undoubtedly due to the unusually high densities of *Pseudocalanus* in CEEs 1 and C, especially in the latter half of the experiment.

Discussion

Using a simulation model it was demonstrated that the observed phytoplankton populations in the three enclosures were sufficient to precipitate the respective *Pseudocalanus* populations without the need to prolong the physiological changes observed in the CEE 5 *Pseudocalanus*. This implies that the phytoplankton environment in CEE 5 did not favor the development of *Pseudocalanus*. The question is, what happened in CEE 5 between days 1 and 24 to favor the subsequent growth of the larger particle dinoflagellates (*Scrippsiella* sp.) and later diatoms (*Chaetoceros* spp.)?

The CEE 5 total copepod population on day 25 is approximately one fifth of that observed in CEE 1 and CEE C (Fig. 2). This is probably a combined result of first, the physiological effects of mercury on *Pseudocalanus*, and second, the smaller initial population of *Pseudocalanus* nauplii (Table 3). Consequently, CEE 5 is experiencing lower grazing pressure on the phytoplankton over the initial 25 days of the experiment.

The response from the phytoplankton in CEE 5 is interesting. Although the microflagellates show a slight response on day 28 to the lower grazing and pumped sediment nutrients, it is not until day 35 that a marked change in the phytoplankton is observed. The dinoflagellates experience a very high growth rate, increase rapidly, and are then reinforced by the addition of organic and inorganic nutrients on day 38. Vertical profiles of phytoplankton carbon indicate that the CEE 5 dinoflagellate bloom on day 35 starts in the top 3 m, possibly implying that the seed for this bloom was brought to the surface with the sediments on day 25.

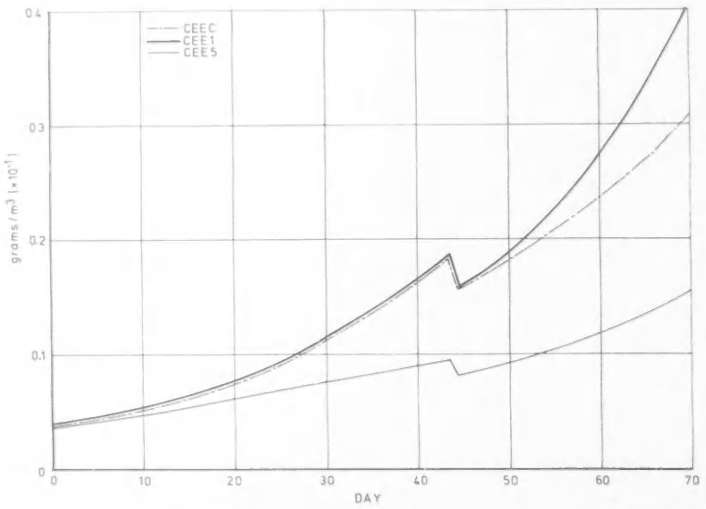

FIG. 12. Simulated salmon biomass (standard run)

$$\left(\text{i.e. weight of one salmon} = \frac{\text{g C/m}^3 * 1300\ \text{m}^3}{37 \text{ or } 45}\right).$$

One interesting but still tenuous hypothesis is that the dinoflagellates formed a cyst as a reaction to a stress (i.e. low nutrients or high mercury levels) enabling them to withstand the high mercury levels. In this cyst form they quickly sank into the sediments from which they were pumped to the surface on day 25. Over the next 10 days conditions were such that they could germinate, enter a period of rapid growth and thereby gain dominance.

Although encysted dinoflagellates have not been reported in the CEPEX bags they have been observed elsewhere. However, the reasons for their formation and eventual germination are still not known, and the problem is being actively researched by others.

The CEE 5 microflagellates, on the other hand, despite the lower grazing pressure, did not respond in the first 30 days indicating a possible stress reaction to mercury in their growth rate.

As for CEE C and CEE 1, the zooplankton grazing pressure maintained the dinoflagellates and diatoms at low levels throughout the experiment. However, with the addition of organic nutrients from the sediments on day 25 the microflagellates in CEE 1 escaped the grazing pressure and experienced rapid growth. An explanation for such a response in CEE 1 but not in CEE C is somewhat tenuous. Low levels of some metals appear to stimulate the growth of microflagellates (e.g. Thomas et al. 1977a). Whether this is actual growth stimulation or a favoring of species with a higher tolerance to low levels of pollutant is not clear. In any case, such a thesis would be an explanation for the observed microflagellate bloom in CEE 1.

In conclusion, therefore, we have demonstrated, using a simulation model, that it is not necessary to hypothesize a long-term effect of mercury on *Pseudocalanus* to explain the low population observed in CEE 5. Instead, it appears that the direct impact could have been short-term, allowing just enough time for the system to establish a different phytoplankton structure.

In other words, it is possible that the direct impact of the 5 $\mu g/\ell$ mercury perturbation was to affect the physiology of *Pseudocalanus*, thereby causing a decrease in grazing pressure over the first 30 days. The indirect or secondary impact was the emergence of dinoflagellates (and later diatoms) as the dominant phytoplankton species. This had a negative feedback impact on *Pseudocalanus* by not providing food suitable for its nauplii.

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Spawning Time and Egg Size of Atlantic Mackerel, *Scomber scombrus*, in Relation to the Plankton[1]

D. M. WARE

Department of Fisheries and the Environment, Fisheries and Marine Service, Marine Ecology Laboratory, Bedford Institute of Oceanography, Dartmouth, N.S. B2Y 4A2

WARE, D. M. 1977. Spawning time and egg size of Atlantic mackerel, *Scomber scombrus*, in relation to the plankton. J. Fish. Res. Board Can. 34: 2308–2315.

The mean date of peak spawning of Atlantic mackerel (*Scomber scombrus*) in the southwestern Gulf of St. Lawrence is July 1 ± 1 wk. This coincides with the maximum abundance of the summer plankton. Mackerel eggs average 1.3 mm in diameter at the beginning of the spawning season in June and decrease steadily to 1.1 mm by mid-August. There is a corresponding trend in the mean size of the plankton, which reach a minimum length in midsummer, and a maximum in winter. This recurring size cycle is as important as the seasonal change in plankton biomass in determining the abundance of suitable food organisms for newly hatched larvae. In an evolutionary sense, the observed reproductive characteristics of mackerel ought to be adaptive since the accurate timing of spawning and the progressive decline in egg size will tend to ensure that the parent stock produces larvae of a suitable size and at the correct time, so they encounter an abundant supply of appropriately sized food organisms.

Key words: reproduction biology, plankton size composition, larval feeding, adaptive behavior, recruitment

WARE, D. M. 1977. Spawning time and egg size of Atlantic mackerel, *Scomber scombrus*, in relation to the plankton. J. Fish. Res. Board Can. 34: 2308–2315.

La fraie du maquereau bleu (*Scomber scombrus*) dans le sud-ouest du golfe Saint-Laurent est à son maximum en moyenne le 1er juillet ±1 sem. Ceci coïncide avec le maximum d'abondance du plancton estival. Les œufs de maquereau bleu mesurent en moyenne 1.3 mm de diamètre au début de la saison de fraie en juin et passent graduellement à 1.1. mm à la mi-août. Il y a une tendance correspondante dans la taille moyenne du plancton, dont la longueur atteint un minimum à la mi-été et un maximum en hiver. Ce cycle à répétition est aussi important que le changement saisonnier de la biomasse planctonique comme facteur d'abondance d'une nourriture suffisante pour les larves nouvellement écloses. Au point de vue évolutionnaire, les caractéristiques de la reproduction du maquereau bleu devraient être adaptives, étant donné que la date précise de la fraie et la diminution progressive de la taille des œufs tendront à favoriser la production de larves de taille adéquate et au bon moment, de sorte que ces dernières trouveront un apport abondant d'organismes de taille appropriée.

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OVER the past decade or so, Fisheries scientists have made two important observations concerning the reproductive biology of marine fish stocks. Cushing (1969) pointed out that the spring spawning season in herring, plaice, and cod is relatively fixed since the standard deviation in the mean date of peak egg production in these species is often less than a week.

It is also well known that summer spawners tend to produce smaller eggs than winter or spring spawners, regardless of whether their eggs are demersal or planktonic (Hempel and Blaxter 1967; Bagenal 1971). This generalization even holds true within a species, as egg size in spring and summer tends to decrease over the reproductive season (Bagenal 1971; Hislop 1975). It is generally believed that this phenomenon is adaptive since large larvae should survive better when either the variability of the food supply is high, or the rate of food production is low (Hempel and Blaxter 1967; Cushing 1967; Blaxter 1969; Bagenal 1967, 1973; Jones 1973). Other workers have pointed out that egg size might also be related to food size as larvae with large yolk sacs seem to use these energy reserves to increase their length so they can consume large planktonic organisms, whereas small larvae are better suited for feeding on smaller particles (Hempel and Blaxter 1967; Jones and Hall 1974; Ware 1975).

The purpose of this study was to determine how

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closely egg diameter and the timing of spawning in Atlantic mackerel (*Scomber scombrus*) are related to the size and abundance of the plankton.

Description of the Study Area

A portion of the northwest Atlantic mackerel stock migrates northward along the coast of Nova Scotia in the spring, and begins to enter the Gulf of St. Lawrence in late May or early June. Most of the population spawns in the area known locally as the Magdalen Shallows, which lies to the southwest of a line drawn between Cape North (Cape Breton Island) and Cape Gaspé (Quebec).

Five surveys of mackerel egg distribution and abundance have been made. In 1972 the entire Magdalen Shallows (about 66,000 km²) was covered from June 5 to July 6. In other years, up to 1977, the sampling program was restricted to St. Georges Bay, which separates the westward side of Cape Breton Island from mainland Nova Scotia. The surface area at low water is 1055 km², so the bay represents about 2% of the spawning ground.

St. Georges Bay is shallow (mean depth of 30 m), but is thermally stratified in summer. The mixed layer extends to about 15 m in July, and 23 m by mid-August. Maximum surface temperatures normally occur in mid-August and regularly exceed 20°C (Fig. 1).

Summer is short in the southwest gulf, as the surface temperature does not reach 10°C until the middle of June, on average, and has cooled to this value by early November. It is during this 150-day period, when the temperature exceeds 10°C, that mackerel spawn and accumulate most of their annual growth increment before they leave for their winter grounds.

In 1973 the sampling program in St. Georges Bay was largely exploratory; however, an estimate of the date of peak egg production was obtained. This article reports some of the major findings for the 1974 and 1975 seasons, as well as some related information from other years.

Sampling Procedure

Plankton samples were collected weekly from mid-June to early September, and at various intervals thereafter, from a random grid of stations (13 in 1974, 10 in 1975). At each station three horizontal tows (1/2-m net, 405-μm mesh) were made simultaneously at surface, 5 m and 10 m over 1 naut. mile (15 min at 4 knots). At the end of each tow a bathythermograph was cast, followed by a vertical plankton haul (1/2-m net, 80-μm mesh). The samples were preserved in a 5% solution of formalin.

The horizontal samples were fractionated to determine the size composition of the plankton. The preserved material was washed through a stack of four screens with a mesh size (top to bottom) of 1050 μm, 860 μm, 602 μm, and 405 μm. The material on each screen was then weighed and sorted visually for fish eggs and larvae. All ichthyoplankton were identified, counted, and measured. Whenever possible the entire sample was examined; if this was not practical, it was reduced with a plankton splitter after weighing, and then sorted.

The vertical hauls, which will be referred to as the 80-μm plankton, were graded into six size fractions: the four noted above plus a 253-μm and 80-μm fraction. The material on each screen was weighed but was not examined, since it generally contained few eggs and larvae.

There are two advantages in fractionating the samples: (i) the recovery of ichthyoplankton was found to be considerably more efficient, and (ii) this simple grading technique provided a quantitative measure of the mean size of the plankton over the sampling period.

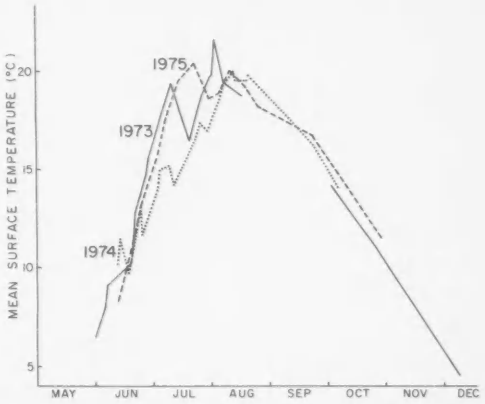

FIG. 1. Average surface water temperature (°C) in St. Georges Bay, Nova Scotia, 1973–75.

Results

Mackerel Spawning Cycle and Egg Size

Fixed date spawning — Mackerel eggs normally appear near the sea surface during the 1st wk in June, when the temperature is about 9°C, and are seldom found after mid-August. This pattern has not changed since the first quantitative survey in 1915 by the Canadian Fisheries Expedition (Dannevig 1919). According to the results obtained in St. Georges Bay, including the two most reliable historical estimates, peak spawning occurs on average on July 1 ± 1 wk (Table 1). At that time the surface water temperature varies between 11 to 15°C.

In 1974 both the surface warming and peak spawning were significantly delayed (Fig. 1). In spite of this variation, however, Table 1 indicates that the reproductive period for mackerel is just as predictable as it is for the spring spawners discussed by Cushing (1969).

During 1974 and 1975 the length of the spawning season and particularly the date of peak egg production coincided with the maximum concentration of the 80-μm plankton (Fig. 2). Mackerel eggs hatch in about 5–7 days at 11 to 14°C. So the peak production of larvae occurred about June 30 in 1975 and July 14 in 1974. By comparison, the biomass of the 80-μm size fraction (of the 80-μm plankton), which is probably the most important food supply for the yolksac larvae reached a maximum on July 7 in 1975, and

TABLE 1. Date of peak spawning of Atlantic mackerel in the southern Gulf of St. Lawrence.

Year	Date	Day	Mean surface temp. °C	Source
ca. 1850–70	July 1–15	ca. 189	?	Goode (1884)
1915	June 30	ca. 181	?	Dannevig (1919)
1972	June 27	178	12.8	Lambert, T. C. (unpublished data)
1973	June 27	178	13.2	This study
1974	July 9	190	14.2	This study
1975	June 23	174	11.8	This study
Mean	July 1	182	13.0	
95% C.L.	June 24–July 8	175–189	11.4–14.6	
SD	—	6.5	1.0	

remained quite high during the entire spawning period in 1974. Considering the unusual hydrographic conditions in 1974, the near synchronous timing of maximum egg production with the generally high abundance of the summer plankton is quite remarkable.

Temporal decline in egg size — The decline in the diameter of mackerel eggs in St. Georges Bay, and elsewhere in the southern Gulf is shown in Fig. 3. In view of the time of spawning, the trend in egg size turns out to be inversely correlated with water temperature (Fig. 4).

It is striking just how closely the average egg diameters measured by Dannevig (1919) over 60 yr ago agree with the recent observations. Indeed, the only conclusion one can draw from these data is that we are witnessing a well-established phenomenon, where the size of eggs produced by the parent stock

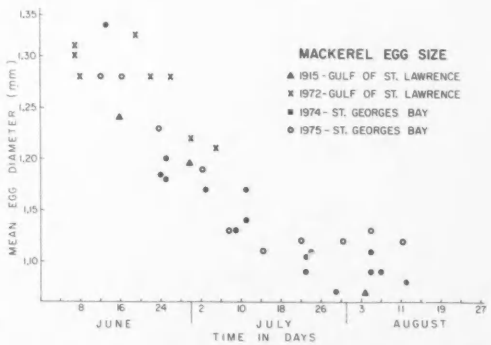

FIG. 3. Temporal decline in diameter of mackerel eggs over the spawning season in St. Georges Bay, and elsewhere in the southern Gulf of St. Lawrence. Means are based on at least 10 measurements. Although the standard errors are not given they average about ± 1 to 2% of the mean value. 1915 measurements were made by Dannevig (1919).

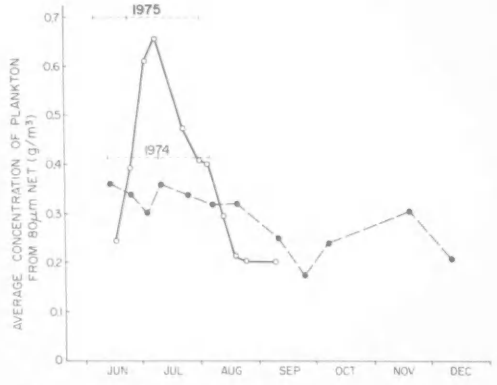

FIG. 2. Relation between time of peak spawning of Atlantic mackerel in St. Georges Bay and biomass of 80-μm-net plankton (1974 solid circles; 1975 open circles). Horizontal dashed lines indicate duration of spawning season in the same years. Vertical lines roughly half way through the season in each case denote date of peak egg production.

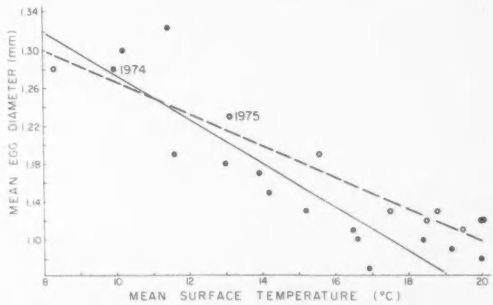

FIG. 4. Relation between egg diameter and surface water temperature in St. Georges Bay. In both years there is a significant linear correlation between variates:
1974 (solid circles, solid line):
$y = 1.50 - 0.023T, r = -0.88, P < 0.01$;
1975 (open circles, dashed line):
$y = 1.44 - 0.017T, r = -0.95, P < 0.001$;
Both years combined:
$y = 1.44 - 0.018T, r = -0.89, P < 0.001$.

TABLE 2. Change in the size and age composition of the mackerel stock in St. Georges Bay in 1976. The mean age was estimated by transforming the Von Bertalanffy growth equation: Hence age (yr) = $\left[\ln\left(\frac{40.0}{40.0 - L_t}\right) \Big/ 0.304\right] - 1.155$.

Date	Length–Range (cm)	Mean length (cm)	Age range (yr)	Mean age (yr)
June 23	29–38	32.7	3–8+	4.5
June 28	21–41	32.9	1–10+	4.5
July 5	21–33	29.7	1–5	3.3
July 15	18–41	31.0	1–10+	3.7
July 21	19–38	22.9	1–8+	1.6
Aug. 11[a]	21–35	25.2	1–6	2.1
Aug. 17	21–26	23.0	1–2	1.7
Aug. 25	21–29	24.0	1–3	1.9

[a]All mature fish were spent.

is closely associated with the solar calender and local hydrographic conditions.

It was once believed that seasonal trends in egg diameter could be attributed solely to variations in temperature and salinity. Recent evidence, however, indicates that most of the variation is of biological origin. Bagenal (1971) noted that the oldest fish are often the first to appear on the spawning grounds and usually produce somewhat larger eggs than recruit spawners. In addition, Hislop (1975) has conclusively shown that the eggs shed at the beginning of the season by individual whiting are both larger and heavier than those shed later.

According to the local fishermen the large "spring" mackerel are the first to appear in the southwest gulf. Table 2 summarizes the length-frequency data for the 1976 spawning season, and confirms that the mean size and age of the population is indeed largest at the beginning of the summer. Thereafter, the mean age decreases as the older fish leave the bay and are replaced by recruit spawners (about 3 yr old or 30 cm) and immature fish.

The ovaries of mature mackerel also contain a wide size range of oocytes. So the potential exists, as in whiting, for egg size to diminish as successive batches are shed over the season. Both observations suggest that the trend in mackerel egg size has a biological basis.

COMPOSITION OF THE PLANKTON

Seasonal variation in species abundance — The 405-μm plankton of St. Georges Bay is dominated by four species of calanoid copepods: *Tortanus discaudatus*, *Temora longicornis*, *Centropages typicus*, and *Calanus finmarchicus*. Throughout May to December in 1973 these species numerically represented 32–79% of all the particles retained by the 405-μm mesh nets, including pelagic fish eggs.

The succession in the relative abundance of these species, and several other plankters that become important for short periods of time is summarized in Table 3. In 1973 barnacle cypris and *Calanus finmarchicus* dominated the late spring (May) plankton until the water began to warm. These species were then replaced by smaller copepods, principally *Centropages typicus*, and *Temora longicornis*. With the onset of autumn *Tortanus* and *Calanus* increased in abundance and by December accounted for roughly 75% of the community. It is worth noting that fish eggs of all species represented 24% of the number of particles caught at the surface in late May, and a remarkable 60% in June and July (Table 3).

Seasonal variation in mean size of the plankton — This change in the plankton species composition suggests that there is a recurring seasonal cycle in particle size. Although I emphasize that the estimated mean sizes given in the last column of Table 3 represent a nominal, rather than a real length, they confirm that the particle size of the plankton community tends to a minimum in midsummer and increases to a maximum in winter. An identical trend occurred in the vertical samples, which were taken over 2 yr in St. Georges Bay and at a station 10 miles off the northern tip of Prince Edward Island (Fig. 5).

Considering the known effects of water temperature on the size at maturity of marine organisms, it is not surprising to find that the mean length of the plankton is also inversely correlated with water temperature (Fig. 6). In fact this relationship partly explains why smaller plankters were more abundant in June and July of 1975 relative to the previous summer (Fig. 5), which was much colder.

Abundance of the 80-μm plankton — It can be shown from the observed variation in the plankton size composition that the number of food organisms available to recently hatched larvae is determined as much by the particle size dynamics of the plankton

TABLE 3. Proportion of various zooplankton retained by the 405-μm surface net during 1973 in St. Georges Bay, Nova Scotia (cf. Willey 1919). The mean size was calculated by weighting the maximum lengths of the dominant species (Brodskii 1950; Hardy 1959) by their proportion in the sample.

Month	Species	Proportion of sample by number	Maximum length (mm)	Weighted mean size (mm)
May	Cirripede cypris	0.29	0.5	
	Calanus finmarchicus	0.19	4.1	1.8
	Temora longicornis	0.11	1.2	
	Tortanus discaudatus	0.09	1.7	
	Fish Eggs	0.24	—	
June/ July	*Temora longicornis*	0.15	1.2	
	Tortanus discaudatus	0.14	1.7	1.5
	Centropages typicus	0.03	1.5	
	Fish Eggs	0.60	—	
Aug.	*Centropages typicus*	0.40	1.5	
	Temora longicornis	0.28	1.2	1.4
	Acartia sp.	0.12	1.0	
	Tortanus discaudatus	0.08	1.7	
	Fish Eggs	0.01	—	
Oct.	*Tortanus discaudatus*	0.36	1.7	
	Temora longicornis	0.16	1.2	
	Centropages typicus	0.11	1.5	1.8
	Pseudocalanus minutus	0.07	1.6	
	Calanus finmarchicus	0.05	4.1	
	Acartia sp.	0.03	1.0	
	Fish Eggs	<0.01		
Dec.	*Tortanus discaudatus*	0.51	1.7	
	Calanus finmarchicus	0.24	4.1	3.3
	Chaetognatha	0.08	12	
	Temora longicornis	0.03	1.2	
	Fish Eggs	<0.001	—	

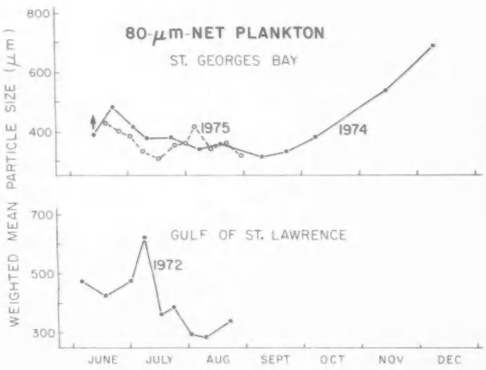

FIG. 5. Temporal trend in the size of the 80-μm-net plankton. A mean length was calculated by weighting the mesh size of the six screens used to fractionate the plankton by the average biomass on each screen. The sample identified by the arrow indicates that this measurement is somewhat underestimated, since several large ctenophores were removed before the sample was fractionated. After mid-June ctenophores become an insignificant component of the community.

as it is by their biomass. For example, between June 13 and August 20, 1974, the average plankton biomass fell by a factor of 1.1 (Fig. 2), while the weight of an average sized particle (assuming weight $\propto$ length^3) decreased 1.6 times (Fig. 5). The result of these two opposing tendencies was a 1.4 fold increase in particle abundance. By comparison, in 1975 the plankton mass increased by a factor of 2.8 times between June 16 and July 7 (Fig. 2), whereas the weight of an average sized particle decreased by the same amount (Fig. 5). So the total number of organisms increased about 8 fold in 21 days.

Link between egg size and food size — The results show that mackerel eggs and the plankton diminish in size over the same time scale. Although it does not necessarily follow that these events occur in phase, the fact that they do (Fig. 7) indicates how well the reproductive biology of mackerel is adapted to the changing structure of the larval food supply.

Table 4 confirms that the length of the first feeding larvae is indeed linked to the size composition of the plankton. Newly hatched mackerel vary between 2 to 4 mm, depending upon egg diameter and probably

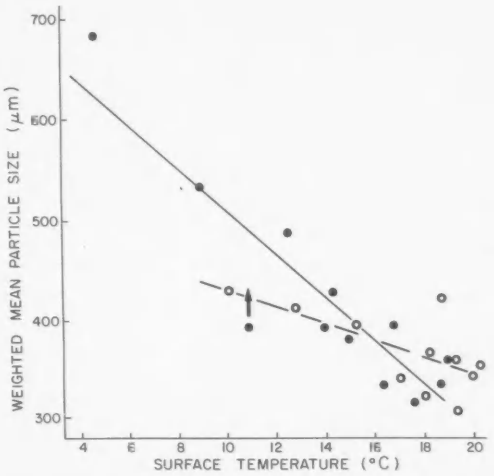

FIG. 6. Trend in mean size of the 80-μm-net plankton in relation to water temperature (°C) in St. Georges Bay. Regressions:
1974 (solid circles, solid line):
$y = 721.08 - 21.71T, r = -0.90 P < 0.001$;
1975 (open circles, dashed line):
$y = 514.11 - 8.52T, r = -0.67, P < 0.05$;
Both years combined:
$y = 657.46 - 16.9T, r = -0.84, P < 0.001$.

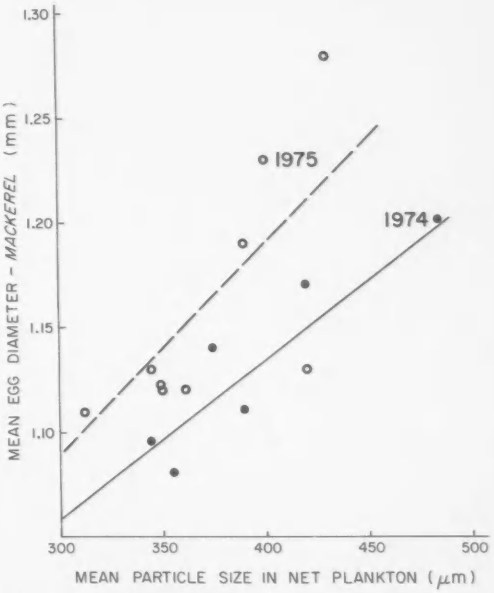

FIG. 7. Relation between mackerel egg diameter and mean size of the 80-μm-net plankton. Regressions:
1974 (solid circles, solid line):
$y = 0.83 + 7.59 \times 10^{-4}X, r = 0.89, P < 0.02$;
1975 (open circles, dashed line):
$y = 0.78 + 1.03 \times 10^{-3}X, r = 0.73, P < 0.05$;
Both years combined:
$y = 0.86 + 7.64 \times 10^{-4}X, r = 0.65, P < 0.01$.

temperature. Since the number of 2-mm larvae caught in relation to the number of recently spawned eggs in the water column at the same time varies inversely with the mean egg diameter (Table 4), it follows from Fig. 7 that the average size of the yolksac larvae changes in phase with that of the plankton throughout the summer.

TABLE 4. Change in the proportion of newly hatched (2 mm) mackerel larvae in relation to the diameter of stage 1 eggs in St. Georges Bay during the 1974 spawning season. Correlation coefficient = −0.88 where $Y = aX^{-b}$.

Date	No. 2-mm larvae	
	No. stage 1 eggs (Y)	$\bar{X}$ egg diameter (mm) (X)
June 14	0.0003	1.32
June 25	0.0160	1.18
July 4	0.0135	1.14
July 11	0.0181	1.15
July 29	0.0050	1.11
Aug. 8	0.0830	1.09
Aug. 13	0.1471	1.08

Discussion

This study is not the first to show that the dimensions of pelagic fish eggs are correlated with water temperature during the spawning season. Southward and Demir (1973) reported the same phenomenon for the Cornish pilchard. They also noted that "the close correspondence in seasonal trends of egg diameter, yolk mass, and oil globule indicate that the cause must be sought in changes influencing the oocyte stage in the ovary, and not in an immediate response of the egg to conditions after spawning."

It should be emphasized that I use the term "fixed date spawning" rather loosely. It is simply a convenient way of stating that some fish stocks have evolved a mechanism that causes the gonad to mature at roughly the same time each year to within an accuracy of, say, 2 wk. Indeed, the controlling biochemical reactions in mackerel seem to ensure that the southern Gulf of St. Lawrence stock reaches a maximum state of maturity between June 24 to July 8. However, abnormal hydrographic events, as in 1974, indicate that peak spawning occurs later than usual if the spring warming progresses slowly.

These observations suggest that, in the event of both short- and long-term climatic change, the stock could synchronize its reproductive cycle and egg diameter with the size dynamics of the plankton by spawning at a fixed temperature. These relationships do not necessarily indicate cause and effect; the point is simply that water temperature carries

some information about the current size composition of the larval food supply. Indeed, it has been shown that the summer of 1974 was much colder than 1975, yet the mean length of the plankton at the same temperature was similar in both years (Fig. 6).

From the point of view of longer term variations, the plankton species composition has not changed markedly in the vicinity of St. Georges Bay since the first quantitative study was made in 1915. Willey (1919) referred to the mixture of *Tortanus discaudatus*, *Temora longicornis* and *Centropages sp.* inhabiting sections of the southern Gulf in summer as the "Souris *Tortanus* plankton." His use of this phrase aptly reflects the fact that this group of neritic copepods occurred almost exclusively in Northumberland Strait and off the western shore of Cape Breton Island.

Although the factors affecting the size structure of the plankton are poorly understood, it is clear that several processes are involved. First, there is the general seasonal replacement of species in the southwest gulf, which alternates between a *Calanus* and *Tortanus* community in winter, and a microcalanoid community in summer. Second, superimposed over this, the size composition is changing continuously in accordance with the life cycles of different species. In view of the enormous number of larvae produced by marine organisms, the average particle size of a population must decline whenever reproduction occurs synchronously over a short period of time. Presumably the mean length will begin to increase after the completion of the spawning cycle, at a rate that depends on the unique survival and growth functions of each generation within a species, until the next breeding period when the cycle is repeated. Since different populations do not reproduce in phase, and since their generation times, and probably the frequency of reproduction are directly related to water temperature, the mean particle size of the community must change with the seasons.

The association between this cyclic variation in the plankton size composition and the reproductive season of mackerel implies that fixed date spawning and the trend in egg size are really inseparable adaptations. Various studies have shown that small fish larvae have a more restricted range in the size of food organisms they can eat than large larvae (Marak 1960; Sherman and Honey 1971). Thus, it seems spawning time in mackerel has evolved so that peak hatching occurs near the summer maximum of zooplankton abundance, while the decline in egg diameter ensures that the parent stock produces larvae of the right length, at the right time, which are well adapted to begin feeding on the existing size composition of the plankton.

Besides this decisive link between a year-class and its food supply, there are at least two other factors that might account for much of the known seasonal variations in egg diameter. Blaxter and Hempel (1963) suggested that this phenomenon is adaptive in herring as it results in the production of large larvae in winter, which are clearly better suited to survive the rigorous feeding conditions at that time. I have also argued elsewhere that the observed trends might be adaptive in view of seasonal differences in the mortality rates of pelagic eggs and larvae (Ware 1975).

Using a simple model of density-dependent growth and mortality, it was shown that females that produce a large number of small eggs, of the right size, during summer ought to have more of their progeny survive the 1st yr of life than females producing large eggs. On the other hand, since the death rate in the sea varies inversely with the size of a particle, small eggs should experience a high mortality during the cold months of the year, when the incubation period is long. As a result, the optimal balance between egg size and maximum survival shifts to favor large ova in winter and spring. Together, these three selective forces probably account for much of the evolutionary basis for variations in egg diameter.

In addition to such general considerations, the reproductive characteristics of mackerel have more immediate implications in terms of the problem of recruitment, since they bring up the question of what might happen to a year-class if reproduction were poorly timed, or if the size of the newly hatched larvae got significantly out of phase with the size composition of their food supply. The St. Georges Bay results are far from being conclusive on this point. But they do suggest that mackerel are probably well enough adapted to their environment so that the spawning time will rarely be so poor as to result in a critical period in the classical sense of Hjort (see May [1974] for a recent review). Although the early larval stage is important, recruitment is surely determined by a combination of factors, which operate throughout the 1st yr of life, rather than by a single, decisive event shortly after hatching. In fact the accurate timing of spawning in mackerel and the associated trend in egg size have probably evolved to minimize the occurrence of precisely this kind of catastrophe in the very early life history.

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Temperature and Water Velocity Effects on the Swimming Performances of Young-of-the-Year Striped Mullet (*Mugil cephalus*), Spot (*Leiostomus xanthurus*), and Pinfish (*Lagodon rhomboides*)[1,2]

ROGER A. RULIFSON

Department of Zoology, North Carolina State University, Raleigh, N.C. 27607, USA

RULIFSON, R. A. 1977. Temperature and water velocity effects on the swimming performances of young-of-the-year striped mullet (*Mugil cephalus*), spot (*Leiostomus xanthurus*), and pinfish (*Lagodon rhomboides*). J. Fish. Res. Board Can. 34: 2316–2322.

Swimming performances of young-of-the-year striped mullet (*Mugil cephalus*), spot (*Leiostomus xanthurus*), and pinfish (*Lagodon rhomboides*) were tested by examining the combination of physical endurance and swimming behavior to provide information on potential fish entrainment and impingement problems at industrial intakes. Tests were conducted at three temperatures (15–25°C) and six water velocities (12–48 cm/s). Fish lengths ranged from 1.4 to 7.0 cm TL. Fish tested at higher temperatures exhibited increased time for steady swimming and for impingement avoidance. Temperature was also positively correlated with maximum swimming speeds and with the number of bursts performed during drift–burst activity (drifting with the current and returning upstream with a burst of swimming). Increased water velocities resulted in decreased times of steady swimming and impingement avoidance, and reduced drift–burst activity. Larger fish avoided impingement longer and had faster maximum swimming speeds; however, smaller fish showed stronger rheotaxis and swam steadily for longer periods at equal water velocities. Abnormally heavy mullet and spot had reduced capabilities for position maintenance (steady swimming) which may decrease their ability to avoid impingement.

Key words: swimming speeds, temperature, water current, impingement, behavior, mullet, spot, pinfish

RULIFSON, R. A. 1977. Temperature and water velocity effects on the swimming performances of young-of-the-year striped mullet (*Mugil cephalus*), spot (*Leiostomus xanthurus*), and pinfish (*Lagodon rhomboides*). J. Fish. Res. Board Can. 34: 2316–2322.

Nous avons étudié la performance de nage de jeunes de l'année de *Mugil cephalus*, *Leiostomus xanthurus* et *Lagodon rhomboides* en observant l'endurance physique et le comportement natatoire. Ces essais ont été faits dans le but de connaître les problèmes d'aspiration et de collision à l'entrée des prises d'eau industrielles. Les essais ont été faits à trois températures (15–25°C) et à six vitesses d'eau (12–48 cm/s). La longueur des poissons variait entre 1.4 et 7.0 cm LT. Les poissons testés aux températures élevées sont plus lents à atteindre une nage uniforme et à éviter les collisions. On a de même trouvé une corrélation positive entre la température et les vitesses de nage maximales et le nombre d'échappées effectuées au moment de l'activité dérive–échappée (dérive avec le courant et retour en amont avec poussée de nage). Une augmentation de vitesse de l'eau entraîne une diminution du temps requis pour atteindre une nage uniforme et éviter les collisions, ainsi qu'une diminution de l'activité dérive – échappée. Les grands poissons évitent les collisions plus longtemps et ont des vitesses de nage maximales plus grandes; cependant, les petits poissons montrent un rhéotactisme plus fort et nagent à une vitesse uniforme durant de plus longues périodes pour de mêmes vitesses d'eau. Les individus exceptionnellement lourds de *Mugil* et de *Leiostomus* sont moins capables de maintenir leur position (nage uniforme), ce qui peut diminuer leur aptitude à éviter les collisions.

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STRIPED mullet (*Mugil cephalus*), spot (*Leiostomus xanthurus*), and pinfish (*Lagodon rhomboides*) are important components of the estuarine fish fauna along the coast of the Carolinas. As adults, mullet and spot are valuable to the commercial and sport fisheries, and pinfish are important as forage fish. Immature fish of these species use the estuaries as a nursery, appearing during the late fall and early

[1]Based on portions of a thesis submitted in partial fulfillment of the requirements for the M.Sc. degree at North Carolina State University.

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winter months and remaining throughout late summer.

This study was designed to test the swimming performances of these species to provide information on potential entrainment and impingement problems. Physical endurance and swimming behavior of fish influence how they may respond to natural currents as well as to currents created by industrial intake and outfall structures. The use of a long-chambered test apparatus (relative to fish size) permitted the fish to exhibit behavioral responses to water flow while swimming. These responses are considered to be more natural than similar studies which force fish to swim in shorter test chambers.

Materials and Methods

Juvenile fish were collected from the Newport River estuary near Beaufort, North Carolina, with a seine; postlarval forms were caught in a channel net (Lewis et al. 1970) modified by wing extensions and an open-topped collecting box. Acclimation and testing were conducted with a recirculating seawater system located in a controlled temperature room at North Carolina State University at Raleigh. Salinity of 32‰ and a 12-h photoperiod were maintained throughout the experiment.

Test Apparatus

The test apparatus (Fig. 1), modified from Beamish (1966), consisted of a transparent tube containing a 10-cm section of cylindrical baffles and a swimming chamber 120 cm long. The chamber was blocked at both ends with 1.5-mm mesh plastic screens. The downstream (rear) screen was electrified by a platinum wire connected to a 6-V battery and manual switch; this was used to stimulate impinged fish. Rings marked on the tube circumference at 20-cm intervals served as visual cues for the fish and as reference guides for the investigator. The apparatus was immersed in a fiberglass tank; water was drawn through the apparatus by a propeller powered by a variable speed motor.

Current velocity was monitored by a calibrated pressure-drop tube inserted 5.5 cm behind the rear screen. Areas of reduced water velocity which may affect fish swimming performance were eliminated by use of the fine-meshed screens; these created a flattened velocity profile of statistically uniform microturbulence. The profile was determined by calculating Reynolds number, a dimensionless quantity applied to liquids flowing through cylinders (Schlichting 1968).

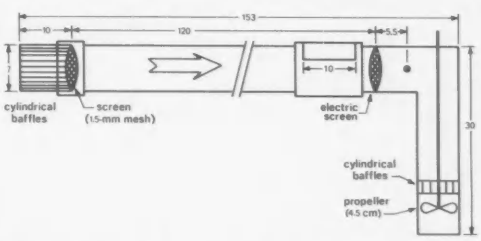

FIG. 1. Schematic drawing of test chamber used for the experiments. Dimensions are expressed in centimetres.

Variables Measured

Four variables were recorded for each test: (1) Steady Swimming Time (SST) was the length of time a fish maintained its position at a given water velocity; (2) Time To Impingement (TTI), total time elapsed from start of test until the fish became impinged for 15 s or more on the rear screen, included the steady swimming time and drift–burst activity (drifting with the current and returning upstream with a burst of swimming); (3) Burst Speed was considered to be the maximum observed speed against a current — it occurred only during drift–burst activity. Burst speeds were calculated by observing the distance the fish swam against the current and the time it took to cover that distance. The observed values were placed into the formula

$$\frac{\text{burst distance (cm)}}{\text{no. of seconds}} + \text{test velocity (cm/s)} = \text{burst speed (cm/s)}.$$

Burst speed (centimetres per second) was then divided by the total length of the fish (centimetres) to obtain swimming units expressed as body lengths per second (L/s). These units permitted the development of comparative data among species and among size classes within species, (4) Maximum Swimming Speed (MSWS) was considered to be the water velocity at which the fish did not maintain a steady position for longer than 30 s (Boyar 1961). The MSWS was determined for those fish which completed a 30-min test without being impinged and was measured by subjecting them to velocity increments of 9 cm/s at 30-s intervals.

Test Procedures

During 1974 and 1975, 1027 fish were tested in 621 observations. The availability of young-of-the-year fish of each species in the estuary determined the period of testing (mid-November through May for spot, and January through July for striped mullet and pinfish). Tests were conducted at 15, 20, and 25° C after acclimation to the test temperature by a 1 deg C change per day for a minimum of 7 days. Water flowing through the holding and acclimation tanks did not exceed 3 cm/s.

The fish were fed 30 min prior to testing; test fish were then selected at random from the holding tank and placed into the swimming chamber. After allowing the fish to explore the chamber for 15 min, a 6 cm/s flow was provided until it oriented upstream. Flow was then gradually increased until the test velocity, randomly selected from 12, 16, 21, 30, 39, and 48 cm/s, was reached. If the fish was impinged on the electrified rear screen before the end of 30 min, the test was terminated and TTI was recorded. If the fish swam for 30 min without impingement, it was then tested for maximum swimming speed. Each fish was tested only once; total fish length and wet weight were recorded after testing.

In analyzing the data, temperature, velocity, length, and weight were each tested for significance ($\alpha = .05$) and positive or negative correlation to the dependent variables (TTI, SST, MSWS, and average burst speeds) by a simple linear regression. Stepwise linear regression was used to determine the "best fit" model for each dependent variable (Draper and Smith 1966).

TABLE 1. Mean time to impingements (seconds) of juvenile striped mullet, spot, and pinfish (size range: 1.4–7.0 cm TL) at six velocities and three temperatures. The number of tests and standard deviation per test (in parentheses) are given below each time. *No tests performed.

Species	Temp (°C)	Velocity (cm/s) 12	16	21	30	39	48
	15	1800	1617	1800	1264	771	21
		8(0)	13(452)	6(0)	6(839)	7(962)	11(19)
Mullet	20	*	1800	1669	1800	1417	884
			7(0)	11(434)	10(0)	11(689)	9(909)
	25	*	*	1800	1800	1705	1276
				10(0)	13(0)	12(329)	12(782)
	15	1800	1418	357	335	64	35
		7(0)	9(758)	6(711)	13(611)	10(61)	13(43)
Spot	20	1669	1470	1018	908	879	228
		13(470)	11(692)	14(845)	11(805)	12(880)	11(529)
	25	*	1690	1393	561	751	379
			14(412)	12(739)	13(769)	13(866)	15(607)
	15	1800	1388	496	127	26	18
		11(0)	13(783)	12(790)	9(231)	14(35)	7(34)
Pinfish	20	1800	1671	1047	970	821	247
		12(0)	14(481)	9(894)	10(795)	13(844)	11(563)
	25	*	1800	1800	1641	1061	1312
			11(0)	9(0)	11(526)	14(886)	12(728)

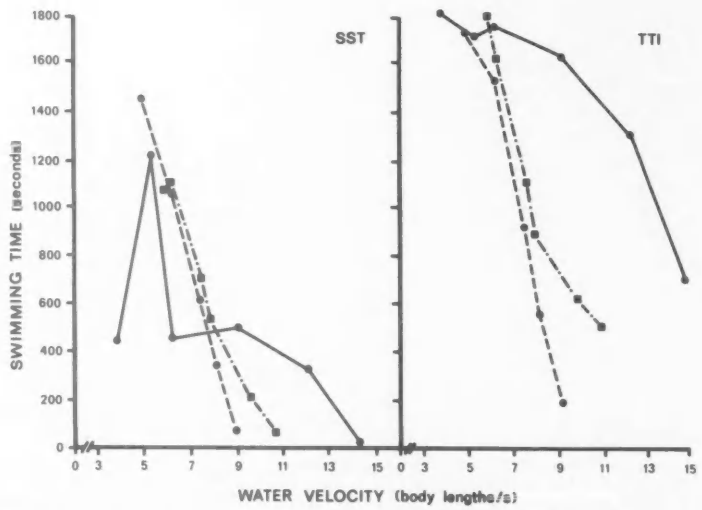

FIG. 2. Effect of velocity on sustained swimming and time to impingements of mullet (●), spot (○), and pinfish (■). SST) Steady Swimming Time; TTI) Time To Impingement.

Results

MULLET

Temperature and velocity of the water were the most significant factors for predicting time to impingement (Table 1, Fig. 2). TTI values were positively correlated with temperature and fish length, and were negatively correlated with water velocity. Individuals heavier than average were able to avoid impingement for longer periods (Table 2).

The steady swimming time of striped mullet decreased with water velocities above 5 L/s (Table 2, Fig. 2) and fish length (Table 2). Abnormally heavy individuals also had reduced SST values (Table 2).

TABLE 2. Swimming performance analysis. Each species and groups within species are shown. Individual significance was determined by linear regression on the dependent variable. Positive and negative correlation is indicated by (++) or (−−) when significant at the 1% level, and (+) or (−) at the 5% level. Non-significance is indicated by (+NS) or (−NS). "Best fit" model was chosen by stepwise regression. Temp = temperature; VEL = water velocity; TL = total fish length; WT = wet weight of the fish; SST = steady swimming time; TTI = time to impingement; MSWS = maximum swimming speed; ABS = average burst speed (by fish); NBURST = number of bursts per fish per test.

Species	Dependent variable	No. of OBS. (N–I)	Singular significance & correlation to dep. var.				Model showing "Best Fit"	*F* value	Significance	R^2	C.V.
			Temp	Vel	TL	WT					
	SST	169	+NS	−−	−−	−	Temp-Vel-TL WT	10.31	.0001	.200	147.03
	TTI	169	++	−−	++	++	Temp-Vel	60.98	.0001	.422	45.64
Mullet	MSWS	79	++		++	++	Temp	40.49	.0001	.341	19.83
	ABS	131	+	++	++	++	Vel	98.14	.0001	.430	28.42
	NBURST	169	++	−−	+	+	Temp-Vel	20.56	.0001	.198	135.83
	SST	202	+NS	−−	−−	−	Temp-Vel-TL	53.85	.0001	.448	96.13
	TTI	202	+	−−	−−	−−	Temp-Vel-TL	68.25	.0001	.507	68.19
Spot	MSWS	77	+		++	++	TL	243.07	.0001	.762	20.75
	ABS	63	+	++	+NS	+NS	Temp-Vel	17.22	.0001	.361	16.37
	NBURST	201	+NS	−NS	−NS	−NS					
	SST	193	++	−−	−NS	+NS	Temp-Vel-TL	38.20	.0001	.376	102.06
	TTI	193	++	−−	+NS	+	Temp-Vel-WT	76.69	.0001	.548	53.21
Pinfish	MSWS	82	++		++	++	TL	364.24	.0001	.818	20.09
	ABS	80	+NS	++	−−	−−	Vel	31.54	.0001	.285	25.59
	NBURST	191	+	−	+NS	+NS	Vel-TL	5.77	.0041	.058	230.86

SST did not appear to be singularly related to temperature ($P > .10$) even though it contributed significantly to the "best fit" model (Table 2).

Maximum swimming speeds of mullet were positively correlated with fish length (Table 2, Fig. 3) and water temperature (Table 2). SST and the previous test velocity of the water did not significantly affect the MSWS ($P > .10$). The average maximum swimming speed for striped mullet was 12.71 L/s (Table 3).

The average burst speed exhibited during drift–burst activity was slightly lower than the average maximum swimming speed (Table 3), although some mullet were capable of swimming up to 20 L/s for several seconds only. Faster burst speeds occurred at higher test velocities while burst activity decreased (Table 2). Average burst speeds and the number of bursts performed were positively correlated with temperature (Table 2), although the stepwise regression analysis did not include temperature in the "best fit" model.

Spot

Time to impingement of spot was significantly related to temperature, velocity, fish length, and individual weight differences (Table 2). TTI values were not consistently higher at any one temperature, although 20°C had the highest average TTI value from all test velocities. Larger fish of this species had reduced TTI values, while smaller individuals (1.7–2.9 cm TL) showed stronger rheotaxis and therefore longer TTI values for equivalent velocities. Heavier spot had greater difficulty in avoiding impingement, although weight did not contribute significantly to the model.

The sustained swimming times of spot were negatively correlated with velocity (Fig. 2) and fish length but increased at higher temperatures (Table 2). Again, the larger spot failed to orient and swim steadily against the current compared to the smaller fish.

The maximum swimming speed of spot was directly related to fish length (Table 2, Fig. 3). Sustained swimming times and previous test velocities did not affect the results of MSWS ($P > .10$). The average maximum swimming speed of spot was 9.39 L/s (Table 3).

TABLE 3. Maximum swimming speeds and burst speeds (±SE) of mullet, spot, and pinfish.

Species	*n*	Avg MSWS (L/s)	*n*	Avg burst speed (L/s)
Mullet	79	12.71±0.387	131	11.08±0.301
Spot	77	9.39±0.219	63	9.52±0.242
Pinfish	82	9.40±0.215	80	9.42±0.325

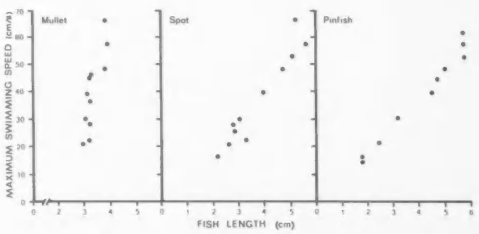

FIG. 3. Maximum swimming speed as related to total fish length.

Average burst speeds approximated the average maximum swimming speed (Table 3) and were positively correlated with temperature and water velocity (Table 2). Most spot tested did not exhibit drift–burst activity.

Pinfish

Time to impingement and sustained swimming times were positively correlated with temperature (Table 1, Table 2) and negatively correlated with water velocity (Table 2, Fig. 2). Smaller fish appeared to be more rheotactic than the larger fish and responded to currents by swimming steadily for longer periods. Heavier individuals had longer impingement avoidance times but shorter sustained swimming times.

The maximum swimming speed of pinfish was directly correlated with total fish length and temperature (Table 2, Fig. 2), although length was the only variable chosen by stepwise regression analysis. The average maximum swimming speed of pinfish (9.4 L/s) approximated the average MSWS of spot (Table 3).

Average burst speeds of pinfish exhibited during drift–burst activity were faster at higher test velocities and temperatures (Table 2); consequently, the number of bursts performed decreased. The average burst speed (9.42 L/s) was slightly higher than the maximum swimming speed, but was lower than burst speeds for spot or mullet (Table 3).

Discussion

Swimming Endurance

Beamish (1966) defined swimming endurance as the length of time a fish maintained its position against a current of known velocity, with the assumption that the swimming speed was equal to the water velocity. In this study, time to impingement (TTI) was also a measure of swimming endurance which reflected both physical strength and behavioral response by the combination of sustained (steady) and drift–burst swimming activities. Thus this study did not attempt to test the total length of time a fish could physically endure steady swim-

ming, but rather how long a fish would respond to a range of water velocities by swimming steadily. This would seem to be a more natural criterion of performance than one of forced swimming.

There may be a critical swimming speed threshold at which fish may prefer to maintain a relative position in a current of water by swimming steadily against the flow. For some fishes this threshold may be about 3–4 L/s (Bainbridge 1960), although Blaxter (1969) reported that some salmonids and clupeids can maintain speeds of 4 or more L/s for indefinite periods. The sustained swimming response in mullet and spot was best about 5–6 L/s; below these speeds the three species did not respond well to test velocities.

Maximum Swimming Speeds

Maximum swimming speed varies with the length of time that a speed must be maintained (Bainbridge 1962; Brett 1964). For longer periods, Larimore and Deuver (1968) observed 20–25-mm smallmouth bass swimming in excess of 10 L/s for at least 3 min. Larval walleye and perch, however, could not sustain currents of 10 L/s even for a few minutes (Houde 1969). In this study, most juvenile mullet (2.5–6.5 cm) sustained maximum swimming speeds of at least 12.7 L/s for 30 s, with values of juvenile spot (1.7–7.0 cm) and pinfish (1.4–6.5 cm) averaging approximately 9.4 L/s.

For brief periods, Bainbridge (1958) predicted the maximum speed for most fish less than 1 m long to be approximately 10 L/s. However, Hunter (1972) reported that very brief bursts (0.1–0.2 s) of larval *Engraulis mordax* reached values of 25 L/s or faster, with average burst speeds closer to 15 L/s. In this study, estimates of burst speeds of mullet and pinfish during velocity changes (in testing for maximum swimming speed) were determined by using the lower velocity to calculate burst speed. From these estimates it appears that some juvenile mullet and pinfish are capable of swimming over 20 L/s for approximately 0.8–2 s. Juvenile spot were slower, with fastest burst speeds approaching 14 L/s.

This study indicated that temperature is highly significant ($P < .01$) when analyzed by linear regression (against the dependent variables maximum swimming speed and burst speed) for mullet, spot, and pinfish (Table 2). However, results from numerous studies have indicated that temperature has a minimal effect on maximum swimming capabilities. Brett (1964) reported that temperature influence on locomotor metabolism of young sockeye salmon is negligible for burst speeds of approximately 4 to 10 L/s. Herring, tested for burst speeds lasting .5–1 min, did not exhibit consistent effect of temperature over a range of 5–18°C (Blaxter and Dickson 1959). Blaxter and Dickson also reported no obvious correlation between temperature and average maximum swimming speeds of herring.

Performance Against Imposed Velocities

Prediction of fish swimming performance to imposed velocities in field situations is impossible without prior knowledge of the behavior and physical abilities of each fish species. Physiologically, a juvenile fish swimming against an imposed velocity may be expected to avoid impingement or entrainment at intake structures for an indefinite period of time by escaping or until complete exhaustion sets in. Behaviorally, however, this same fish may not actively swim against the imposed current if the velocity (relative to the fish) is greater or less than 3–6 L/s. In this situation, individuals of certain species may drift or swim with the current until reaching the intake structure, thus becoming entrained or impinged. These responses to currents may be modified in schooling individuals due to social interaction and hydrodynamic efficiency of schooling fish (Breder 1965).

Lyon (1904) and Keenleyside and Hoar (1954) reported that fish depend upon visual or tactile cues and labyrinthine reflexes for spatial orientation. Fish without this orientation (due to darkness or murky water) may not be able to sense the speed of the current properly and may be entrained or impinged, regardless of size. Therefore, visual and/or tactile cues may aid in decreasing the numbers of juvenile fish impinged or entrained at industrial intakes.

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Relative Toxicity of Free Cyanide and Dissolved Sulfide Forms to the Fathead Minnow (*Pimephales promelas*)[1]

STEVEN J. BRODERIUS, LLOYD L. SMITH JR., AND DAVID T. LIND[2]

Department of Entomology, Fisheries and Wildlife, University of Minnesota, St. Paul, Minn. 55108, USA

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The relationship between pH and acute toxicity of free cyanide (i.e. HCN + CN^-) and dissolved sulfide (i.e. $H_2S + HS^- + S^{2-}$) to the fathead minnow (*Pimephales promelas*) at 20°C was determined for pH values ranging from about 6.8 to 9.3 and 6.5 to 8.7, respectively. The 96-h median lethal concentrations (LC50s) of free cyanide and molecular HCN were little different and fairly constant within the pH range 6.8–8.3. Beyond this, to pH 9.3 the values diverged markedly, with the free cyanide LC50s increasing and the HCN LC50s decreasing. Except for some increase with rise of pH from about 6.5 to 7.1, the 96-h LC50 concentrations of molecular H_2S decreased linearly and by approximately fourfold as the pH increased from 7.1 to 8.7. The 96-h LC50 concentrations of dissolved sulfide in corresponding equally toxic solutions increased logarithmically as pH increased from 6.5 to 8.7. Acute toxicities to fathead minnows of free cyanide and dissolved sulfide do not depend entirely on the concentration of ambient molecular HCN or H_2S. Change in toxicity of the molecular forms with pH was evaluated by two gill-permeability theories. The likelihood of certain chemical changes occurring at the gill surface or the possible penetration of the gill by both molecular and anionic forms present in the test solutions at different pH's was evaluated. Increased apparent toxicity of molecular HCN or H_2S with elevated test pH is believed to result from the CN^- and HS^- anions penetrating the gill epithelium, though less readily than do the molecular forms, and enhancing the toxicities of these solutions as the pH increases.

Key words: toxicology, hydrogen ion concentration, bioassays, lethal limits, gill-permeability theories

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Nous avons déterminé la relation entre le pH et la toxicité aiguë du cyanure libre (i.e. HCN + CN^-) et du sulfure dissous (i.e. $H_2S + HS^- + S^{2-}$) pour le tête-de-boule (*Pimephales promelas*) à 20°C et à des pH allant d'environ 6.8 à 9.3 et de 6.5 à 8.7 respectivement. Les concentrations létales médianes après 96 h (CL50) de cyanure libre et de HCN diffèrent peu et sont assez uniformes dans les limites de pH de 6.8–8.3. Passé ce point, jusqu'à un pH de 9.3, les valeurs diffèrent notablement, la CL50 de cyanure libre augmentant et celle de HCN diminuant. Sauf pour une certaine augmentation avec l'élévation de pH allant d'environ 6.5 à 7.1, les CL50 après 96 h de H_2S moléculaire diminuent suivant une fonction linéaire et d'environ quatre fois à mesure que le pH passe de 7.1 à 8.7. Les CL50 après 96 h de sulfure dissous en solutions également toxiques augmentent suivant une fonction logarithmique à mesure que le pH passe de 6.5 à 8.7. La toxicité aiguë pour le tête-de-boule du cyanure libre et du sulfure dissous ne dépend pas entièrement de la teneur en HCN ou en H_2S moléculaire ambiant. Nous proposons deux hypothèses de perméabilité des branchies pour évaluer le changement de toxicité des formes moléculaires en fonction du pH. Nous examinons la probabilité de certains changements chimiques à la surface de la branchie ou la pénétration possible dans la branchie des formes tant moléculaire qu'anionique présentes dans les solutions d'essai à différents pH. L'apparente augmentation de toxicité du HCN ou du H_2S moléculaires en fonction de l'augmentation du pH

[1]Paper No. 9874, Scientific Journal Series, Minnesota Agricultural Experiment Station, St. Paul, Minn. 55108, USA.
[2]Present address (D.T.L.): Copper–Nickel Studies, Environmental Quality Council, State Planning, Minneapolis, Minn. 55413, USA.

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dans les essais résulterait de la pénétration des anions CN^- et HS^- dans l'épithélium branchial, moins facilement toutefois que les formes moléculaires, et augmentant la toxicité de ces solutions à mesure que le pH augmente.

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THERE are several fish body surfaces where exchange of gases and ions between blood and water can occur, but the gill epithelium is recognized as the primary site. It is also generally accepted that ions have less toxicity than do more lipid-soluble, unionized molecules. Ions are less toxic because of difficulty in penetration of strongly charged membranes. The relatively large hydrated ions are absorbed or repulsed by the charged protein surfaces of the membranes. Acute toxicity to fish of solutions containing free cyanide (i.e. HCN and CN^-) or dissolved sulfide (i.e. H_2S, HS^-, and S^{2-}) is mainly attributed to the toxic action of molecular HCN or H_2S and is largely independent of the concentrations of the CN^- or HS^- and S^{2-} anions, which are considerably less toxic than the molecular forms (Doudoroff and Katz 1950; Bonn and Follis 1967; Doudoroff 1976).

Two gill-permeability theories have been proposed to explain the observed change in toxicity of ammonium salt solutions to aquatic organisms with change of pH. Lloyd and Herbert (1960) postulated that only NH_3 is effective; and, rather than the pH value of the test solution being important in determining the toxicity of ammonium salts to fish, it is the pH value of the solution at the gill surface that controls the concentration of NH_3 at the penetration site. Gill surface pH supposedly depends on the amount of respiratory CO_2 excreted by the fish that lowers the pH value of the solution in contact with the gills. Tabata (1962) states that the ammonium ion penetrates membranes and has a measurable toxicity considerably less than that of the molecular form which penetrates more readily. Lloyd and Herbert (1960) and Tabata (1962) also suggested that their theories for ammonium salts were generally applicable to weak bases and could presumably even be used to assess the toxicity of other poisons, such as weak acids, that are affected by pH changes within the range tolerated by fish.

Because the toxicity of weak acids and bases is known to be pH dependent, this study was designed to define the change in tolerance limits of the fathead minnow to free cyanide and dissolved sulfide forms as a function of pH. Applicability of the above gill-permeability theories for explaining the bioassay results was also tested.

Materials and Methods

Test Water and Fish

The experimental well water used in all bioassays had a total alkalinity and hardness of 235 and 220 mg/ℓ as $CaCO_3$, respectively. A comprehensive analysis of the water was reported by Smith et al. (1976).

Juvenile fathead minnows (*Pimephales promelas*) were used as test organisms. Minnows used in all the bioassays were cultured in the laboratory from a stock originally obtained from the U.S. Environmental Protection Agency's Environmental Research Laboratory in Duluth, Minnesota. The minnows were reared under 16-h illumination each day in 30-ℓ glass aquaria receiving a continuous supply of well water at 25°C with a pH of approximately 7.9. We believed that the inbred laboratory strain of fish would have a more uniform sensitivity to the toxicants not too different from that of other stocks tested at different times and that the possibility of disease could be reduced and/or treatment stress minimized by not using wild stocks. Six lots of fish were tested during separate 15-wk periods in each of the cyanide and sulfide series. The fish were all approximately 13 wk old at testing, had mean total lengths of 30.8 and 30.1 mm, and had mean wet weights for survivors of 0.289 and 0.293 g in the cyanide and sulfide bioassays, respectively. The fish were fed unrestricted rations of Oregon Moist and Glencoe pelleted food twice daily until 1 day before exposure to the toxicants.

Testing Conditions

The 96-h toxicity bioassays were performed in three identical diluter and test-chamber units, each including one control and four treatment chambers. The experimental glass chambers measured 50 × 25 × 20 cm high and contained 20 ℓ of test solution. The intermittent water delivery and toxicant introduction systems were modifications of those described by Brungs and Mount (1970) and Mount and Warner (1965), respectively. Flow through each chamber was at the rate of 500 ml/min, affording 99% replacement in about 3 h.

Temperature of the test water was 20°C. Aeration in the head reservoirs maintained dissolved oxygen concentrations in the test chambers near 7.5 mg/ℓ. Each chamber was illuminated for 12 h daily with a 40-W incandescent bulb 25 cm above the chamber. Stock solutions of sodium cyanide or sodium sulfide were prepared with reagent grade chemicals and deionized water.

Fathead minnows acclimated to 20°C for 1 wk were randomly distributed among the 12 treatment and 3 control chambers until there were 10 or 20 fish in each. A sulfuric acid or sodium hydroxide solution was dispensed into the head reservoirs to control the pH of the test water. Fish were acclimated to the desired pH and diluter apparatus for 2–3 days before introduction of the toxicants. The relationships between pH and acute toxicity of free cyanide and dissolved sulfide forms were determined at 20°C for pH values ranging from about 6.8 to 9.3 and 6.5 to 8.7, respectively.

Chemical Analysis

During each bioassay, water temperature, dissolved oxygen (DO), and pH in each test chamber were measured daily. Alkalinity was determined daily in each control

chamber by potentiometric titration with a standard 0.02 N H_2SO_4 solution. Dissolved oxygen was measured with a galvanic-type membrane electrode meter and pH with a corning Model 112 glass-electrode meter standardized with two primary buffers (APHA et al. 1975). The free carbon dioxide concentrations in test solutions were derived by the nomographic method (APHA et al. 1975) from the pH, temperature, bicarbonate alkalinity, and total filtrable residue.

Free cyanide concentrations in each chamber were determined daily by the pyridine–pyrazolone colorimetric method (APHA et al. 1971). Dissolved sulfide concentrations, which were determined to be essentially the same as total sulfide concentrations, were measured in treatment chambers at least twice daily. Water samples taken from the center of each test chamber were stabilized with zinc acetate and analyzed for sulfide by the methylene blue colorimetric procedure (APHA et al. 1971). The concentration of molecular HCN or H_2S was calculated for each free cyanide or dissolved sulfide determination using the daily pH and temperature measurement and the pK equilibrium constants (i.e. $-\log K$) calculated by using the equations

$$pK_{HCN} = 3.658 + 1662/T \text{ (S. Broderius unpublished data)}$$
$$pK_{H_2S} = 3.122 + 1132/T \text{ (Broderius and Smith 1977)}$$

where T is temperature in degrees Kelvin. The ratio [HCN]/[free cyanide] or [H_2S]/[dissolved sulfide] is taken to be equal to $1/(1 + 10^{pH - pK_a})$ assuming [S^{2-}] to be negligible and when omitting the second equilibrium constant for dissolved sulfide. When both the molecular HCN or H_2S and free cyanide or dissolved sulfide concentrations are expressed in the same units and as the molecular form, then free cyanide or dissolved sulfide times the appropriate factor will equal molecular HCN or H_2S.

Statistical Analysis

Estimates of the concentration of cyanide or sulfide most likely to cause 50% mortality (LC50) after 96 h of exposure were made from lines fitted mathematically by the BMDO3S log-probit analysis computer program (Dixon 1973). All the data from toxicity tests conducted at a specific pH were composited for probit analysis. The 96-h LC50 values for both free cyanide and HCN or dissolved sulfide and H_2S were calculated at each pH. The 95% confidence intervals for LC50 values were computed according to formulas proposed by Litchfield and Wilcoxon (1949) and Finney (1971). Chi-square tests were applied to each group of data for tests conducted at a specific pH to determine variability and acceptability. When heterogenity was indicated, the appropriate adjustment in the 95% confidence intervals for LC50 values was made (Litchfield and Wilcoxon 1949).

Results and Discussion

The test conditions and log-probit analysis of composite test results grouped according to pH are summarized in Tables 1–3. The 96-h LC50 concentrations of free cyanide and molecular HCN differed little and were fairly constant within the pH range 6.8–8.3. Beyond this, to pH 9.3 the values diverged markedly with the free cyanide values increasing and the HCN values decreasing.

Except for some increase with rise of pH from about 6.5 to 7.1, the 96-h LC50 concentrations of molecular H_2S decreased as the pH increased. These values in micrograms per litre H_2S ranged from 57.2 at pH 7.1 to 14.9 at pH 8.7. Within this pH range a 0.1 unit increase in pH was calculated by linear regression ($r = -0.994$) to result in a 2.7 $\mu g/\ell$ decrease in the 96-h LC50 value of molecular H_2S. As test pH increased, the 96-h LC50 concentrations of dissolved sulfide in corresponding equally toxic solutions increased logarithmically.

The unexpected result for the sulfide experiments performed at a pH of about 6.5 may be due to an interaction between sulfide and the relatively high CO_2 concentration in the test solutions. The LC50 values for H_2S may be relatively constant over the pH range of about 6.5–7.1 and when the free CO_2 level is held constant.

Lloyd and Herbert's Theory

According to the theory of Lloyd and Herbert (1960), the toxicity of cyanide and sulfide solutions to the fathead minnow should be increased by depression of pH at the gill surface due to respiratory excretion of CO_2. This change in toxicity results from the conversion of CN^- or HS^- anions to molecular HCN or H_2S in the solution in contact with the gills. The magnitude of this effect depends upon the concentration of free CO_2 present in solution and the shifting of the CO_2-bicarbonate-carbonate chemical equilibrium. When the concentration of free CO_2 in water is very low (high pH), the addition of respiratory CO_2 considerably reduces the pH value at the gill surface. As the level of free CO_2 rises in the bulk of the solution the pH change becomes less. Theoretically, the pH at the gill surface can be calculated from the bicarbonate alkalinity, temperature, free CO_2 concentration in the test solution, and the free CO_2 excreted by the gills of fish by use of the standard nomographic method for determination for free CO_2 (APHA et al. 1975). The increase in concentration of excreted CO_2 in the respiratory water (as milligrams CO_2 per litre) was estimated by Lloyd and Herbert (1960) by means of the equation

$$\text{Increase in } CO_2 = DO \times RQ \times \frac{\text{mol wt } CO_2}{\text{mol wt } O_2} \times \frac{P}{100} \quad (1)$$

where DO is the dissolved oxygen concentration of the water in milligrams per litre, RQ is the respiratory quotient of the fish, and P is the percentage of oxygen removed from the respiratory water by the fish. Kutty (1968) has determined that the RQ is essentially unity when freshwater fish are spontane-

TABLE 1. Mean test conditions for composite free cyanide and dissolved sulfide bioassays; SD in parentheses.

Test pH	Temp °C	DO mg/ℓ	Alkalinity mg/ℓ $CaCO_3$		Free CO_2 in test solution[a]	
			Bicarbonate	Total	mg/ℓ	mm Hg
		Cyanide series				
6.830 (0.028)	20.1 (0.12)	7.65 (0.06)	96	96	28.0	12.4
7.559 (0.041)	20.0 (0.02)	7.56 (0.09)	193	193	11.0	4.9
8.286 (0.034)	20.0 (0.01)	7.66 (0.06)	240	240	2.5	1.1
8.672 (0.067)	20.1 (0.09)	7.59 (0.09)	229	244	1.0	0.44
8.974 (0.068)	20.0 (0.12)	7.71 (0.10)	214	243	0.47	0.21
9.262 (0.091)	20.2 (0.09)	7.63 (0.12)	206	250	0.24	0.11
		Sulfide series				
6.462 (0.070)	20.0 (0.05)	7.62 (0.08)	63	63	44.0	19.5
7.101 (0.030)	20.0 (0.04)	7.66 (0.09)	128	128	20.5	9.1
7.698 (0.036)	20.0 (0.20)	7.65 (0.07)	198	198	7.9	3.5
8.151 (0.030)	20.0 (0.11)	7.49 (0.24)	229	229	3.2	1.4
8.430 (0.018)	20.0 (0.05)	7.55 (0.11)	234	238	1.7	0.75
8.693 (0.014)	20.1 (0.10)	7.49 (0.11)	234	243	1.0	0.44

[a]Free CO_2 evaluated by nomographic method (APHA et al. 1975). Assuming $K = H_2CO_3/P_{CO_2}$ and $\log K = -1.41$ at 20°C and 1 atm, then 1 mg/ℓ CO_2 = 0.444 mm Hg CO_2 tension (Stumm and Morgan 1970, p. 148).

TABLE 2. Analysis by the log-probit method of the results of fathead minnow bioassays of cyanide at 20°C with tests grouped according to pH; 95% confidence limits in parentheses.

Test pH	Log-probit regression analysis[a]			HCN 96-h LC50 μg/ℓ as HCN	Free cyanide 96-h LC50 μg/ℓ as HCN
	Treatments[b]	α	β		
6.830	6	−23.80	13.76	124 (106–144)	—
		−23.82	13.76	—	124 (107–144)
7.559	7	−23.47	13.81	115 (102–130)	—
		−23.60	13.82	—	117 (102–135)
8.286	6	−27.37	15.52	122 (115–128)	—
		−28.00	15.54	—	133 (126–140)
8.672	9	−33.46	18.88	109 (105–113)	—
		−34.59	18.64	—	133 (128–138)
8.974	17	−16.52	10.68	104 (96–112)	—
		−16.44	9.83	—	152 (140–165)
9.262	10	−28.73	17.55	83 (80–87)	—
		−28.57	15.29	—	157 (142–173)

[a]For equation $Y_i^{\wedge} = \alpha + \beta (\log X_i)$ when $Y_i^{\wedge}$ is the maximum likelihood probit value of percent mortality and X_i is log cyanide concentration as μg/ℓ HCN (Dixon 1973).
[b]Number of cyanide concentrations in the regression analysis.

ously active in nearly air-saturated water. Since the CO_2 is excreted along the surface of the lamellae, a pH gradient may be present in the gills. Lloyd and Herbert proposed that the average pH be taken as that which is produced when half the total amount of CO_2 excreted is at equilibrium with the carbonate system. An analysis of the cyanide and sulfide bioassay data by their procedure is summarized in Table 4. The apparent change in toxicity of HCN and H_2S with change of test pH could mathematically best be reconciled by Lloyd and Herbert's theory if the fathead minnow removes about 10 and 55% of the dissolved oxygen from the respiratory water for the cyanide and sulfide bioassays, respectively. Any other dissolved oxygen utilization values would have resulted in larger standard deviations for the calculated HCN and H_2S concentrations at the gill surface necessary to give the 96-h LC50 responses at different pH values (Table 4).

The above proposed explanation of the toxicity to fish of weak acids and bases and its relation to pH may not be appropriate. First, Lloyd and Herbert assumed that the utilization of oxygen initially present in water passing over the gills of rainbow trout (*Salmo gairdneri*) was about 80%. Recent studies have shown that the percent oxygen removed varies among individuals of the same and different species and for a given fish under different conditions and at

TABLE 3. Analysis by the log-probit method of the results of fathead minnow bioassays of sulfide at 20°C with tests grouped according to pH. 95% CL in parentheses.

Test pH	Log-probit regression analysis[a]			H_2S 96-h LC50 $\mu g/\ell$ as H_2S	Dissolved sulfide 96-h LC50 $\mu g/\ell$ as H_2S
	Treatments[b]	α	β		
6.462	11	− 9.85	8.78	49.2 (45.1–53.7)	—
		−10.64	8.65	—	64.1 (58.7–70.0)
7.101	8	−14.12	10.88	57.2 (52.6–62.1)	—
		−18.57	11.09	—	133 (123–145)
7.698	8	−18.26	14.70	38.2 (32.8–44.5)	—
		−39.54	18.73	—	239 (219–260)
8.151	6	−31.70	25.98	25.8 (24.7–27.0)	—
		−52.98	22.10	—	420 (394–448)
8.430	6	−30.67	28.19	18.4 (17.5–19.4)	—
		−52.31	20.94	—	546 (483–616)
8.693	9	−11.07	13.68	14.9 (13.0–17.2)	—
		−40.23	15.56	—	806 (726–895)

[a]For equation $Y_i^{\wedge} = \alpha + \beta$ (log X_i) when $Y_i^{\wedge}$ is the maximum likelihood probit value of percent mortality and X_i is log sulfide concentration as $\mu g/\ell$ H_2S (Dixon 1973).
[b]Number of sulfide concentrations in the regression analysis.

different times. According to a review by Shelton (1970) almost all reported utilization values are <80% under nearly ideal environmental conditions. Utilization is usually <50% when there is hypoxic stress (Holeton and Randall 1967; Davis and Cameron 1971). In view of the stress occurring in an acute toxicity bioassay, the utilization might even be considerably less than the 55% value necessary to explain Lloyd and Herbert's theory of the sulfide bioassay data. The percentage utilization of dissolved oxygen at the gills of fish in tests performed under nearly identical environmental conditions was calculated to be 5.5 times as great for fathead minnows tested in sulfide solutions as for those tested in the cyanide solutions. This discrepancy is an additional reason why the theory is not appropriate to explain the relation between pH and the toxicity of weak acids to fish.

The RQ of fish may not remain constant throughout the duration of an acute toxicity test. According to Kutty (1968, 1972) and Kutty et al. (1971), the in vivo RQ can increase upon marked reduction of DO from accumulation of lactic acid in the tissues and consequent release of CO_2 from the bicarbonate reserve, which take place when metabolism is partially anaerobic. Because of the nature of the toxic action of cyanide and sulfide, a similar response may be expected of fish dying from these poisons. If the RQ does increase, the percentage of available oxygen removed at the gills could decrease and still be accompanied by an increase in CO_2 at the gills necessary to justify Lloyd and Herbert's theory.

A second weakness of the theory is apparent when one examines the manner and amount in which CO_2 is excreted at the gills. According to Dejours et al. (1968), when the RQ is near unity, the changes in CO_2 tension of the water passing over the gills of teleost fish are small. In their experiments with goldfish (*Carassius auratus*) at 25°C this change was <1.0 mm Hg. Holeton and Randall (1967) determined that the P_{CO_2} of the blood in the ventral aorta was greater by about 1.0 mm Hg than that in the dorsal aorta of rainbow trout both in well-aerated water and in a hypoxic environment. Rahn (1966) stated that the change in CO_2 tension of the water at the gills could not be much greater than 5 mm Hg at 20°C, and it could be that great only if nearly all the O_2 in the water passing over the gills was extracted.

The mechanism for the excretion of metabolic CO_2 by freshwater fish includes the catalytic conversion to bicarbonate of some of the CO_2 in the blood by carbonic anhydrase in the gill epithelium (Randall 1970). Therefore, along with the free CO_2 entering the water, bicarbonate passes across the gill epithelium by an active exchange mechanism that involves chloride. Stumm and Morgan (1970) indicated that the hydration-dehydration reaction of $CO_2(aq) + H_2O \leftrightarrows H_2CO_3$ proceeds slowly in water, the establishment of the hydration equilibrium at pH values near 7 requiring many seconds. The formation of CO_2 from the bicarbonate actively excreted by the gill epithelium is also slow. Water is generally considered to pass over the gill epithelium in <2 s, and the hydration of CO_2 and formation of CO_2 from bicarbonate in water is in the order of many seconds. Therefore, the major portion of the rise in P_{CO_2} and ultimate pH shift at equilibrium should occur after the water has left the respiratory surface.

To explain the cyanide and sulfide toxicity bioassay data by the theory of Lloyd and Herbert, the total increase in CO_2 at the gill surface when oxygen utilization is 10 and 55% would need to average

TABLE 4. Average estimated 96-h LC50 concentrations of molecular HCN or H_2S at the fathead minnow gill surface assuming a dissolved oxygen utilization of 10 and 55%, respectively, for the cyanide and sulfide bioassays at 20°C and an RQ of 1.0.

Test pH	Avg free CO_2 at gill[a] mg/ℓ	Avg pH at gill[b]	One-half pH decrease at gill	Ionization factor for gill pH[c]	Free cyanide or dissolved sulfide 96-h LC50, μg/ℓ	HCN or H_2S at gill to give 96-h LC50, μg/ℓ[d]
			Cyanide series			
6.830	28.53	6.82	0.01	0.997	124	124
7.559	11.52	7.52	0.04	0.985	117	115
8.286	3.03	8.19	0.10	0.932	133	124
8.672	1.52	8.50	0.17	0.871	133	116
8.974	1.00	8.68	0.29	0.816	152	124
9.262	0.76	8.81	0.45	0.767	157	120
					Mean	120
					SD	4.2
			Sulfide series			
6.462	46.88	6.41	0.05	0.789	64	50.5
7.101	23.40	7.04	0.06	0.467	133	62.3
7.698	10.79	7.57	0.13	0.205	239	49.0
8.151	6.13	7.87	0.28	0.115	420	48.2
8.430	4.55	8.01	0.42	0.0858	546	46.8
8.693	3.83	8.10	0.59	0.0709	806	57.1
					Mean	52.3
					SD	6.1

[a]Free CO_2 in test solution (Table 1) plus one-half increase in CO_2 at gill surface (Lloyd and Herbert 1960).
[b]Calculated from average free CO_2 at gill, using nomograph for evaluation of CO_2 (APHA et al. 1975).
[c]Factor = $1/(1 + 10^{pH-pK_a})$ when $pK_{HCN} = 9.328$ and $pK_{H_2S} = 6.983$ at 20°C.
[d]Equal to the ionization factor for average pH at the gill times the free cyanide of dissolved sulfide 96-h LC50 concentration.

about 1.0 and 5.7 mg/ℓ or 0.44 and 2.5 mm Hg, respectively. These increases, although physiologically possible, are greater for the sulfide bioassays than those that have been reported in the literature (Randall 1970). The accompanying maximum total pH change necessary for agreement with the theory would need to be 0.9 and 1.2 units for the cyanide and sulfide bioassays at the highest test pH values, respectively. These changes appear to be extreme, since Holeton and Randall (1967) measured a 0.2 pH unit difference between water samples from the buccal and opercular chambers of the rainbow trout. Because of all the above considerations we conclude that the theory of Lloyd and Herbert is not appropriate to explain the relation of toxicity to pH observed in the reported cyanide and sulfide bioassays.

TABATA'S THEORY

With an increase in pH more free cyanide or dissolved sulfide becomes necessary to produce the acute response (Tables 2 and 3). However, the increase in concentration needed is not large enough to maintain a constant 96-h LC50 concentration of molecular HCN or H_2S. If the toxicity of free cyanide and dissolved sulfide is attributable to the molecular component only, the slopes of curves relating the proportion of weak acid present in the molecular form and the toxicity to test pH should be parallel. Inspection of these relationships plotted in Fig. 1 shows that this is not the case over the entire pH range tested. Discrepancy between the curves occurs mainly in the alkaline region, where the ratio of weak acid anions to total acid increases rapidly with rise of pH. Therefore, CN^- and HS^- anions may have a toxicity equal to at least a fraction of the toxicity of the neutral molecules. The theory of Tabata (1962), which assumed that not only the molecular forms but also the ionized fraction can penetrate membranes and have a measurable toxicity, may thus be appropriate for explaining the toxicity of cyanide and sulfide solutions to fish.

The relationship expressing Tabata's theory, where the total toxicity is equal to the sum of the toxicities due to the molecular and ionic forms, can be represented by the equation

$$\frac{C}{LC50} = T_m\,[\text{molecular form}] + T_i\,[\text{ionic form}] \qquad (2)$$

where C is the total concentration of molecular plus ionic forms, 1/LC50 is an expression of total toxicity, and T_m and T_i are the molar toxicities of the molecular and ionic forms, respectively. The ratio between the toxicity of the molecular and ionic forms (T_m/T_i) can be derived from the LC50 determined at one pH and that (LC50′) determined at another pH (pH′). This relationship for weak acids was defined by Tabata as follows:

$$\frac{T_m}{T_i} = \frac{\frac{K}{[H^+]'}\left(1 + \frac{K}{[H^+]}\right)LC50' - \frac{K}{[H^+]}\left(1 + \frac{K}{[H^+]'}\right)LC50}{\left(1 + \frac{K}{[H^+]'}\right)LC50 - \left(1 + \frac{K}{[H^+]}\right)LC50'} \tag{3}$$

where K is the acidic ionization constant. This equation was used to analyze the cyanide and sulfide bioassay data; the calculated T_m/T_i values are presented in Table 5. It was anticipated that the ratios would be fairly constant, that is, independent of the pH. This was essentially the case for the cyanide bioassays, the overall mean ratio being 2.3. The ratios calculated for the sulfide bioassays were somewhat variable but fairly constant when the pH values were between 7.7 and 8.4. The calculated T_m/T_i values within this pH range average about 15 when the value 6.49 is omitted. Therefore, the effective toxicity to the fathead minnow of the HCN and H_2S molecules in solution is apparently about 2.3 and 15 times that of the CN^- and HS^- anions, respectively.

The above equation (3) can be modified to estimate a new LC50′ for a new pH′ from the given pH, LC50, and T_m/T_i values. This relationship for weak acids was defined by Tabata as follows:

$$LC50' = \frac{\left(1 + \frac{K}{[H^+]'}\right)\left(\frac{T_m}{T_i} + \frac{K}{[H^+]}\right)}{\left(1 + \frac{K}{[H^+]}\right)\left(\frac{T_m}{T_i} + \frac{K}{[H^+]'}\right)} \cdot LC50 \tag{4}$$

The predicted LC50′ values (Table 5) for the cyanide bioassays are estimates based on the mean pH and LC50 values for Tests 1 and 2 and a T_m/T_i ratio of 2.3. The predicted LC50′ values for the sulfide bioassays are estimates based on the LC50 experimentally determined at pH 7.7 and a T_m/T_i of 15. As seen in Table 5, the predicted and determined 96-h LC50 values generally show good agreement, but at the highest pH value of the sulfide series (pH 8.7) the determined value for dissolved sulfide is decidedly larger than the one predicted.

The percentages of total toxicity attributable at different pH values to the molecular and ionic forms can be calculated from the expressions $[P_m/\{P_m + P_i(T_i/T_m)\}](100]$ and $[P_i/\{P_i + P_m(T_m/T_i)\}][100]$, respectively, where P_m and P_i represent the proportions of free cyanide or dissolved sulfide in the molecular and ionic forms, respectively. These toxicity relationships (Fig. 2) were calculated assuming T_m/T_i ratios for the cyanide and sulfide bioassays of 2.3 and 15, respectively. The anions contribute a larger proportion of the total toxicity with increasing pH. An appreciable deviation from the theoretical relationship (Line A in Fig. 2) was noted only in the sulfide bioassay series when the pH was relatively high.

To explain more fully the variable relationship between the toxicity of weak acid solutions and pH, the concentration and form of the toxicants not only in the test solutions but also in the body fluids should be considered. Carbon dioxide is known to diffuse readily through tissues, and the CO_2 tension (P_{CO_2}) in blood vessels efferent to the gills of fishes approximates that of the water in the buccal cavity (Stevens and Randall 1967). An increase in CO_2 content of the water thus produces an increased CO_2 content and decreased pH of the blood. Plasma proteins and hemoglobin buffer the H^+ derived from the dissociation of carbonic acid which is formed when CO_2 is hydrated. Albers (1970, fig. 11) showed that for carp (*Cyprinus carpio*), as the blood P_{CO_2} is increased from about 2 to 12 mm Hg, the blood pH decreases from about 7.9 to 7.4. Ferguson and Black (1941) determined that at 15°C, as the blood P_{CO_2} of the carp was increased from 2 to 20 mm Hg, the plasma pH of oxygenated blood decreased from 7.91 to 7.23. A comparable decrease for the rainbow trout (*Salmo gairdneri*) was from 7.66 to 7.15. In a study by Hunn (1972) on the effect of isobornyl thiocyanoacetate (Thanite®) on the blood chemistry of the carp, a decrease in O_2 and glucose utilization and an accumulation of lactic acid resulting from blockage of

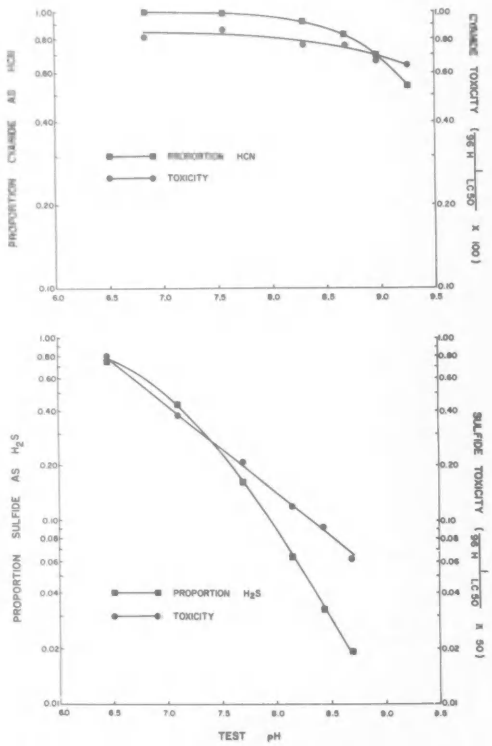

FIG. 1. Toxicity of free cyanide or dissolved sulfide to the fathead minnow and the proportion of each present in the molecular form (as HCN or H_2S) in relation to test pH at 20°C.

the electron-transfer chain by cyanide poisoning were noted. The increase of lactic acid levels was reflected in a decrease of the blood pH from 7.85 in controls to 7.2 in exposed fish. Therefore, the blood pH of fathead minnows exposed to cyanide and sulfide test solutions probably decreased with increasing ambient CO_2 tensions, decreasing test pH, and accumulation of lactic acid in the blood due to poisoning.

It is generally recognized that molecular forms penetrate membranes more readily than charged ions and that blood levels should increase in fish concurrently with increases in ambient concentrations. Since the molecular forms can move across internal tissue barriers more readily than charged ions do, it is assumed that the effectiveness of cyanide or sulfide as an internal poison becomes greater with an increase in the proportion existing in the molecular form (Hewitt and Nicholas 1963). Therefore, a complete explanation of the observed relationship between test pH and cyanide or sulfide toxicity must include consideration not only of the penetration of the gill epithelium, mainly by the molecular forms, but also of variations in degree of internal ionization with changes in blood and intracellular pH associated with changes in internal CO_2 tension and lactic acid concentration.

A change in the permeability of the gills to molecular HCN or H_2S may also contribute to the apparent change in toxicity, but a change sufficient to entirely account for the decrease in molecular form LC50 values, especially in the sulfide series of tests, is most unlikely. This explanation is also deemed not appropriate, since the toxicity of the cyanide forms was relatively constant over a wide range in pH.

At the blood pH of the fish in all the cyanide test solutions, high percentages of the free cyanide that penetrated the gills must have existed as HCN. Thus, when the calculated T_m/T_i ratio of 2.3 was used, the predicted 96-h LC50 values for free cyanide bioassays showed good agreement with the determined values (Table 5). For sulfide, predicted values based on a T_m/T_i ratio of 15 and tests at pH 7.7, levels at which the blood pH is assumed to be near that of the test solution, good agreement be-

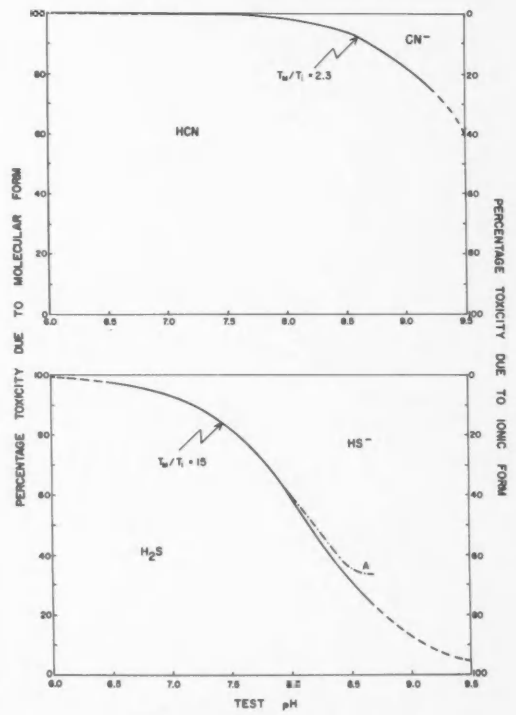

FIG. 2. Relations between pH and the percentages of total toxicity attributable to the molecular and ionic forms of cyanide and sulfide in bioassays with the fathead minnow at 20°C. Deviation of experimental data from the theoretical relationship is indicated by Line A.

TABLE 5. Calculated T_m/T_i ratios and predicted LC50 values for cyanide and sulfide bioassays at different pH values.

Test no.	pH	T_m/T_i ratio for test number[a]					Free cyanide or dissolved sulfide 96-h LC50, $\mu g/\ell$	
		1	2	3	4	5	Determined	Predicted[b]
				Cyanide series				
1	6.830	—	—	—	—	—	124	120
2	7.559	0.18	—	—	—	—	117	120
3	8.286	5.75	−1.40	—	—	—	133	125
4	8.672	1.60	3.45	1.01	—	—	133	133
5	8.974	2.51	4.42	2.14	6.08	—	152	145
6	9.262	1.82	2.26	1.63	1.95	1.23	157	162
				Sulfide series				
1	6.462	—	—	—	—	—	64	66
2	7.101	−7.22	—	—	—	—	133	111
3	7.698	17.3	6.49	—	—	—	239	239
4	8.151	16.8	10.2	16.3	—	—	420	412
5	8.430	16.8	11.6	16.6	17.0	—	546	526
6	8.693	22.9	16.9	25.5	35.2	77.3	806	615

[a]Ratio applies to comparison of the test indicated by the test number below with the test at a higher pH whose test number appears in the first column (Equation 4). The K_{HCN} and K_{H_2S} values at 20°C are 4.700×10^{-10} and 1.041×10^{-7}, respectively.

[b]Values based on T_m/T_i of 2.3 or 15, and mean pH and LC50 values of Tests 1 and 2 or of Test 3 for cyanide and sulfide bioassays, respectively.

tween determined and predicted 96-h LC50 values was observed, except at pH >8.4. The apparent anomaly may be due to the pH of the blood having been slightly higher in fish tested in the more alkaline solutions than in those tested at pH 7.7 and 7.9 mg/ℓ free CO_2. In the bioassays at high pH more of the sulfide presumably had to penetrate largely as HS^- ions to produce a toxic effect equal to that produced at pH 7.7. Therefore, a greater amount of dissolved sulfide than that predicted was required to produce the toxic response at the elevated pH. At higher ambient than blood pH values, the presence of an internal H_2S concentration greater than the level in the ambient medium is conceivable; the concentration gradient across the gill surface then would allow some H_2S to move by diffusion from the blood into the water, thus additionally reducing the toxicity of the dissolved sulfide. We therefore conclude that the acute toxicity to fathead minnows of free cyanide and dissolved sulfide does not depend entirely on the concentration of ambient molecular HCN or H_2S, but that the CN^- and HS^- anions penetrate the gill epithelium less readily than do the molecular forms and increasingly enhance the toxicities of these solutions as the test pH increases.

Acknowledgments

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Tests for Association of Transferrin and Lactate Dehydrogenase Phenotypes with Weight Gain in Rainbow Trout (*Salmo gairdneri*)

GARY L. REINITZ[1]

Fish Genetics Laboratory, U.S. Fish and Wildlife Service, Beulah, Wyo. 82712, USA

REINITZ, G. L. 1977. Tests for association of transferrin and lactate dehydrogenase phenotypes with weight gain in rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 34: 2333–2337.

Transferrin (Tf) phenotype was associated with weight gain in 147- and 230-day-old rainbow trout, but no association was found between lactate dehydrogenase (LDH) phenotype and weight gain. A total of 2038 progeny were examined from two different environments. Progeny lots were reared at densities below those known to affect mean fish weights. Differential survival among progeny with respect to their Tf of LDH phenotype was not detected.

Key words: biochemical genetic markers, economic performance, transferrin, lactate dehydrogenase, weight gain

REINITZ, G. L. 1977. Tests for association of transferrin and lactate dehydrogenase phenotypes with weight gain in rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 34: 2333–2337.

Le phénotype transferrine (Tf) est associé au gain pondéral chez des truites arc-en-ciel de 147 et 230 jours, mais nous n'avons pas trouvé de relation entre le phénotype lactate déshydrogénase (LDH) et la gain pondéral. Nous avons examiné un total de 2 038 descendants provenant de deux milieux différents. Les lots de descendants ont été élevés à des densités inférieures à celles reconnues comme affectant le poids moyen des poissons. Nous n'avons pas décelé de différence dans la survie des descendants par rapport à leurs phénotypes Tf ou LDH.

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IDENTIFICATION of biochemical genetic markers associated with characters of commercial importance, such as growth and percentage hatch, in rainbow trout (*Salmo gairdneri*), would be of obvious economic value to fish culturists. For example, specific matings between trout possessing genotypes associated with good growth could produce good growth rates in offspring.

Since tests for association of biochemical genetic markers with other characters require the examination of heteroallelic loci, the possibility of isolating such a marker in rainbow trout seems good. In comparison with other commercially reared fishes, most populations of rainbow trout possess a highly polymorphic genome.

Transferrin (Tf) is a biochemical genetic marker in the serum of rainbow trout that has been associated with a wide variety of characters in other animals. Balakhnin and Solomatina (1970) found a correlation between Tf types and the condition factor and body length of carp (*Cyprinus carpio*). Other characters found to be associated with Tf type are productivity of a population in bream (Kirsipuu et al. 1972), percentage hatch in pigeons (Frelinger 1972), calf weight at time of weaning (Fowle et al. 1967), embryo mortality in chickens (Gilmour and Morton 1971), and milk production in dairy cows (Ashton et al. 1964).

Because of the success of finding an association of Tf types with various characters in other animals and its heteroallelic state in certain rainbow trout populations, I tested for the presence of an association between Tf types with weight gain in rainbow trout. Lactate dehydrogenase (LDH) phenotypes were also recorded for trout red blood cells to test for an association with weight gain.

Materials and Methods

A random sample of 501 rainbow trout of the Fish Lake strain was taken from the McNenny National Fish Hatchery, Spearfish, South Dakota. They were derived from a pool of 100,000 eggs taken from 95 male and 95 female Fish Lake rainbow trout maintained at the Fish Genetics Laboratory (FGL) and shipped to the McNenny NFH as eyed eggs. These trout were reared in raceways supplied with artesian well water at 11°C and were sampled 230 days after fertilization. The Fish Lake strain of rainbow trout

[1]Present address: Diet Development Center, Fish and Wildlife Service, Route 1, Box 205, Spearfish, S. Dak. 57783, USA.

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maintained at the FGL was obtained in June of 1973 as eggs taken directly from ripe females at Fish Lake in central Utah. Fish Lake is a high mountain lake that has had a resident population of rainbow trout since the early 1900s. However, additional rainbow trout have been stocked in Fish Lake over the years but no records of these stockings is currently available.

A sample of 826 fish representing 42 progeny lots of inbred lines maintained at the FGL was taken 230 days after fertilization. Inbred lines were made by the full-sib matings of various combinations of standard reference population (SRP), Fish Lake, Sand Creek, New Zealand, and Donaldson rainbow trout with resultant inbreeding coefficients (F) ranging from .250 to .594 (Table 1). All progeny lots were maintained separately in circular rearing tanks under standardized conditions as described by Kincaid et al. (1976). The water temperature at the FGL is 11 ± 1°C.

An additional sample of 711 fish representing 36 progeny lots of the standard reference population (SRP) maintained at the FGL was taken 147 days after fertilization. Rainbow trout of the SRP were derived by the mixed mating of Donaldson, Sand Creek, and New Zealand strains of rainbow trout in a ratio of about 6:3:1. A pool of 500 adult trout for each year-class of SRP fish is kept at the FGL through randomized matings. The fish sampled in this study were third generation SRP trout and were reared under conditions as described for progeny of the inbred lines.

Transferrin (Tf) phenotypes and individual weights were recorded for all juvenile rainbow trout examined (a total of 2038 trout). Lactate dehydrogenase phenotypes were recorded for inbred lines and SRP progeny. Parental Tf and LDH phenotypes were known for progeny lots reared at the FGL only.

Tf or LDH phenotypic frequencies for pure strains of Donaldson, Sand Creek, and New Zealand rainbow trout used to create the SRP and inbred lines at the FGL are not available.

TABLE 1. History of the 42 progeny lots examined in this study representing the inbred lines maintained at the FGL. Strain abbreviations are as follows: Donaldson — D, standard reference population — SRP, Fish Lake — FL, Sand Creek — SC, and New Zealand — NZ.

Original parental cross (♂ × ♀) (Frequency of cross in parentheses)	Inbreeding coefficient of progeny
FL × FL (10)	.250
SRP × SRP (3)	.250
SRP × FL (6)	.250
FL × SRP (3)	.250
SC × (SC × NZ) (2)	.406
(SC × D) × SRP (1)	.500
(SRP × (SC × D) (1)	.500
SRP × SRP (2)	.500
SC × SC (2)	.500
NZ × NZ (4)	.500
SC × D (1)	.500
SRP × SC (1)	.500
SC × SRP (2)	.500
SRP × NZ (3)	.500
NZ × NZ (1)	.594

The progeny were bled by severing the tail and collecting the blood in heparinized microcapillary tubes. Parent trout were bled by entering the caudal vein posterior to the anal fin with a 22-gauge needle fitted to a heparinized 3-cm³ hypodermic syringe. The whole blood was centrifuged at 2500 rpm (1200 *g*) for 10 min and the plasma decanted and stored at −20°C. The cells were washed twice with 0.9% saline and lysed with distilled water. The lysate was centrifuged at 2500 rpm (1200 *g*) for 10 min and then stored at −20°C.

Horizontal starch-gel electrophoresis was performed in the manner described by Utter et al. (1974). For the separation of Tf, I used a discontinuous buffer consisting of 0.03 M lithium hydroxide–0.19 M borate (pH 8.1) for the electrode trays and 0.05 M citric acid (pH 8.4) mixed in a ratio of 9:1 with the electrode buffer for gels (Selander et al. 1971). A second discontinuous buffer consisting of 0.06 M lithium hydroxide–0.03 M borate (pH 8.6) for the electrode trays and 0.03 M tris–0.005 M citric acid (pH 8.0) mixed in a ratio of 100:1 with the electrode buffer for gels (Ridgway et al. 1970) was used for the separation of LDH. Staining procedures used were as described by Selander et al. (1971).

Body weight is known to be influenced by numbers of fish present in each rearing container (Brauhn et al. 1976). Furthermore, body weight is of primary concern in studies of the relation of weight gain to different phenotypes. Thus, the numbers of fish per container and mean weight in the container are correlated. Correlation of mean weight and number in the 36 families of SRP trout used in this study was tested when fish were 147 days old.

Results

TRANSFERRIN

The six transferrin phenotypes detected in this study (Fig. 1) reflect three codominant alleles (Tf^a, Tf^b, Tf^c) coding for a monomer at a single locus as reported by Utter et al. (1973). Breeding data from SRP trout used in this study support this model; Tf phenotypic frequencies observed in 35 of 36 progeny lots agreed with those expected according to Mendelian inheritance.

Analysis of variance (ANOVA) of individual weights of juvenile rainbow trout classified according to Tf phenotype revealed a significant difference ($P < 0.01$) between classes for all three of the populations tested (Table 2). When Tf phenotypic groups were ranked according to mean weight, the various Tf classes for both inbred lines (postfertilization age 230 days) and SRP trout (postfertilization age 147 days) reared at the FGL were in approximately the same order ($3 > 4 > 6 > 5 > 2 > 1$). However, Tf phenotypic classes of the Fish Lake strain (postfertilization age 230 days) reared at the McNenny NFH exhibited nearly an opposite order when ranked according to mean individual weights ($6 > 2 > 1 > 5 > 3 > 4$). Figure 2 illustrates the association between Tf phenotype and 230-day mean weight for juvenile rainbow trout reared at the McNenny NFH (Fish Lake strain) and the FGL (inbred lines) in differing environments.

TABLE 2. Phenotypes, corresponding mean weights, and phenotypic frequencies for rainbow trout tested and a listing of results of analysis of variance (ANOVA) of individual fish weights classified according to Tf phenotype for each group.

	Fish Lake trout (McNenny NFH)			Inbred Lines (FGL)			SRP (FGL)		
Tf phenotype no. (mean weight in grams) /no. of fish in phenotypic class/	1	(16.0)	/239/	1	(9.8)	/477/	1	(4.0)	/228/
	2	(16.4)	/128/	2	(9.9)	/59/	2	(4.0)	/95/
	3	(15.1)	/20/	3	(14.0)	/6/	3	(5.0)	/14/
	4	(12.3)	/25/	4	(13.7)	/72/	4	(5.0)	/81/
	5	(15.3)	/78/	5	(11.6)	/186/	5	(4.0)	/208/
	6	(19.3)	/11/	6	(11.7)	/26/	6	(4.4)	/85/
Postfertilization age (days)		230			230			147	
ANOVA *F*-test value		3.2			16.6			15.6	
$P <$		0.01			0.005			0.005	

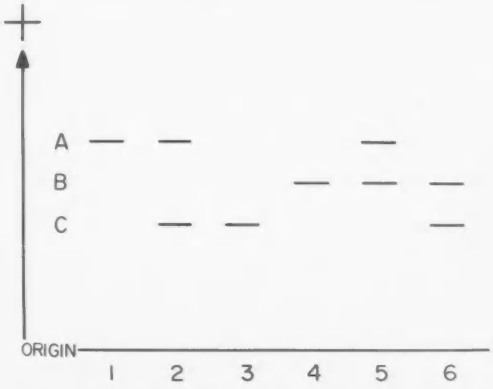

FIG. 1. Diagram of the six transferrin phenotypes resulting from the three transferrin alleles, *A*, *B*, and *C* (Tf^a, Tf^b, and Tf^c).

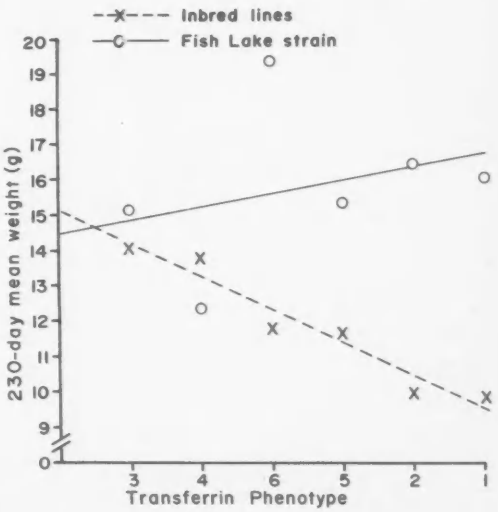

FIG. 2. Mean weight of Tf phenotypic classes of two populations of rainbow trout (inbred lines and Fish Lake strain) at 230 days.

The fact that environments in which fish were reared at the FGL and the McNenny NFH differ, is of no consequence to the conclusions drawn about the association between Tf phenotype and growth. Fish within any of the populations examined (here regarding inbred lines as a single population) were reared under identical environmental conditions. Therefore, any association found to exist between characters within a population is independent of environmental differences existing between rearing facilities for the different populations.

Since density differences could in part explain differential growth between lots reared under otherwise identical conditions, a *t*-test was run on the correlation of mean fish weight with the number of fish per lot. No correlation was found at the 0.05 level of significance in any of the 36 lots of SRP trout tested.

Differential survival with respect to Tf phenotype within the progeny groups was not observed; expected and observed phenotypic frequencies closely agreed. Possible changes in phenotypic frequencies from the parent to the offspring generations were not measured because of preselection of parent pairs for this experiment based on their known Tf phenotypes.

Using Falconer's (1960) measure of allelic dominance, I found the effect of the *A* allele (Fig. 1) on growth strongly dominant over the effects of both alleles *B* and *C* in all three populations tested. Complete dominance ($D = 1.0$) was expressed in two of the six tests. Overdominance was observed between alleles *B* and *C*.

LACTATE DEHYDROGENASE

Three LDH phenotypes were observed in red

blood cell extracts of rainbow trout. These phenotypes reflect two codominant alleles coding for a tetrameric molecule at a single locus, as reported by Williscroft and Tsuyuki (1970) for the livers of rainbow trout. Liver LDH phenotypes are identical with those found in red blood cell extracts in rainbow trout. Breeding data from the present experiment support this model; the observed LDH phenotypic frequencies agreed with those expected according to Mendelian inheritance in all 36 progeny lots of the SRP. This agreement between observed and expected frequencies again indicates that no detectable differential survival in progeny is taking place with respect to the three LDH phenotypic groups observed. Allelic frequencies in the parent population were in agreement with those expected according to Hardy–Weinberg proportions.

Analysis of variance of individual weights of rainbow trout of the inbred lines and SRP group classified according to LDH phenotype showed no difference between classes at the 0.05 level of significance.

Discussion

This study points out the apparent association between different allelic forms of a biochemical genetic locus (transferrin) and a polygenic character (growth) in juvenile rainbow trout. This apparent association was found in two different age-classes of rainbow trout (postfertilization ages 147 and 230 days) and in two different environments (FGL and McNenny NFH). How Tf phenotypic groups rank according to mean weight is not of primary importance. The reversal of rank according to 230-day mean weight of fish with various Tf phenotypes reared in two different environments (Fig. 2) is most likely a result of the sensitivity of the physiological function of biochemical variants to changes in the environment. The most salient finding of this study is simply the existence of an association between Tf phenotype and weight gain.

This apparent association could be explained in several ways. Zschocke and Bezkorovainy (1974) review some of the many papers showing direct associations between Tf phenotype and bacteriostatic and fungistatic activity. These differences were attributed to possible variable ironbinding capacities of various allelic forms of Tf. Therefore, Tf could be directly associated with weight gain if different allelic forms of Tf functioning differentially in iron transport had some direct effect on growth. Secondly, the apparent association between Tf phenotype and weight gain could be explained by the recent cross between genetically distinct populations resulting in the nonrandom association of unlinked loci. This nonrandom association would be reduced in half with each successive generation.

Juvenile rainbow trout of the closed SRP are third generation fish. Therefore, nonrandom association of unlinked loci in this population would already have been reduced to 1/8 of its original magnitude. It seems even less likely that a nonrandom association of unlinked loci would be detected if cross sections of several genetically distinct populations were sampled, provided that these populations had allelic forms of Tf in common. Yet the association between Tf phenotype and weight gain was detected in the inbred lines which are comprised of several genetically distinct lines with diverse historical backgrounds (Table 1). Also, rainbow trout of the Fish Lake strain are descendents of a resident population of a high mountain lake. The majority of fish in this lake have had several generations to approach genetic equilibrium, thus minimizing the chances of detecting a nonrandom association of unlinked loci in the Fish Lake strain.

The association of Tf phenotype and weight gain could also be explained by the linkage of the Tf locus with a gene or gene complex affecting growth. However, the same arguments against nonrandom association of unlinked loci apply to linked loci.

In view of the diverse historical background of the groups of fish examined in this study, the possibility of different Tf phenotypes affecting weight gain directly seems better than other explanations at present. However, more studies will be needed using populations of rainbow trout of diverse origin before such a statement can be made with surety.

Even though no differential survival was detected based on Tf phenotype in the offspring examined, it would be impossible to detect differences in fertility or viability without having extensive random samples of successive generations. Also, it is doubtful that different growth rates would not impart different selective values to fish in a wild environment.

No association was found between lactate dehydrogenase phenotype and weight gain in either the inbred lines or SRP rainbow trout. Robertson (1972) concludes, "The hope of demonstrating an effect on fitness or economic performance of the vast majority of protein variants is likely to prove illusory." I include this statement to emphasize that Tf was selected for investigation because of past studies demonstrating differential selection among Tf variants. Therefore, the chances of finding an association between Tf phenotype and weight gain were much greater than would be expected for the vast majority of other biochemical variants, such as LDH.

To speculate on the application of the findings of this study to fish culture would be premature. However, I hope that this paper will stimulate more intensive studies into the association between Tf phenotype and weight gain in rainbow trout with the subsequent clarification of the practical importance of the findings of this study.

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Artificial Hybrids Between Amur Pike, *Esox reicherti*, and North American Esocids

E. J. CROSSMAN

Department of Ichthyology and Herpetology, Royal Ontario Museum, Toronto, Ont. M5S 2C6

AND JAMES W. MEADE

Pennsylvania Fish Commission, Benner Spring Fish Research Station, Bellefonte, Pa. 16823, USA

CROSSMAN, E. J., AND J. W. MEADE. 1977. Artificial hybrids between Amur pike, *Esox reicherti*, and North American esocids. J. Fish. Res. Board Can. 34: 2338–2343.

Artificial hybrids between *Esox reicherti*, the only species in the family Esocidae that does not occur naturally in North America, and North American esocids were developed. Five of a possible 10 crosses are described in detail. Three crosses failed (those involving the males of *E. niger* and *E. americanus*) for reasons other than methodology, the cross involving females of *E. americanus americanus* was not made, and a fifth cross involving the male of *E. masquinongy* was successful but no data are included. Interspecies fertility was suprisingly high, and an inverse relationship existed between survival of crosses and the difference in potential maximum size of parent species. At least one cross was fertile, and an F_2 generation and backcrosses were developed.

Key words: artificial hybrids, Esocidae, *Esox reicherti*, *Esox masquinongy*, *Esox lucius*, *Esox niger*, *Esox americanus*

CROSSMAN, E. J., AND J. W. MEADE. 1977. Artificial hybrids between the Amur pike, *Esox reicherti*, and North American esocids. J. Fish. Res. Board Can. 34: 2338–2343.

Nous avons développé des hybrides artificiels entre *Esox reicherti*, le seul membre de la famille des Esocidae qui ne soit pas présent naturellement en Amérique du Nord, et des ésocidés nords-américains. Nous décrivons en détails 5 croisements sur un total possible de 10. Trois croisements ne réussirent pas (ceux impliquant les mâles de *E. niger* et de *E. americanus*) pour des raisons autres que la méthodologie, le croisement impliquant les femelles de *E. americanus* a été omis, et un cinquième croisement impliquant le mâle de *E. masquinongy* a été réussi, mais nous n'incluons pas de données. La fertilité interspécifique est étonnamment élevée, avec relation inverse entre la survie des hybrides et la différence de taille maximale potentielle de l'espèce parente. Au moins un croisement est fertile et nous avons produit une génération F_2 et des rétrocroisements.

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PIKES and pickerels (Esocidae) comprise only five species of a single genus, *Esox*, of which three are strictly North American, one is circumpolar, and one is confined to northeastern Asia (Amur River). The group has a fossil history extending back probably to the Eocene (Cavender 1969) and, among esocoids, their karyotypes ($2n = 50$) are the most generalized (Beamish et al. 1971). Morphology and a recent study of their lens proteins (Eckroat 1974) indicate that they fall into two groups: the pikes, *E. lucius*, *E. reicherti*, *E. masquinongy*; and the pickerels, *E. americanus americanus*, *E. a. vermiculatus*, *E. niger*.

In an earlier study Crossman and Buss (1965) described the previously known natural and cultured hybrids of North American species of *Esox*, and described results of an experiment carried out by the Pennsylvania Fish Commission to produce artificial hybrids of all possible reciprocal crosses. The only species of the family not then available was *Esox reicherti* Dybowski, the Amur pike of the USSR and China, which did not, at that time, occur in North America.

The aims of the original study were to add genetic data to the interpretation of the evolution of the species of *Esox*, and to describe characteristics of the various hybrids as an aid in the practical problems of identification and law enforcement resulting from increased interest in using hybrids of some members of the family in sport-fishery management. The first objective was seriously hampered by the

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absence of data on hybrids involving *E. reicherti*. The published data now serve the second objective to only a limited extent because specimens of *E. reicherti* and hybrids between it and North American esocids have been released in at least one body of public water in the United States [Glendale Lake, Cambria Co., Pa., Meade (1977)].

This paper describes the results of an experiment conducted in 1973 at the Union City Hatchery and Benner Spring Research Station of the Pennsylvania Fish Commission, which yielded hybrids between *E. reicherti* and North American esocids and adds to our knowledge of hybridization in this family.

Materials and Methods

Methodology for this experiment was described by Crossman and Buss (1965). Material used in 1973 involved eggs and milt from adult individuals of *E. reicherti* that had been pond-reared at Benner Springs. These adults resulted from eggs that had been sent to Pennsylvania from the USSR in 1968–70. The sources of the North American esocids were as follows: *E. masquinongy* Mitchill — Edinboro Lake, Pa. (Ohio River population); *E. lucius* Linnaeus — Conneaut Lake, Pa. (Allegheny River); *E. niger* Lesueur — Hankins Pond, Delaware River system, Pa.; *E. americanus americanus* Gmelin — tributary of Lehigh River, Pa.; *E. americanus vermiculatus* Lesueur — Allegheny River, Pa.

The hybrids produced consisted of the following 6 of a possible 10 reciprocal combinations (number of individuals involved in this description and range of total length in millimetres in parentheses: *E. reicherti*♂ × *E. masquinongy* ♀ (9; 48–158), *E. reicherti*♀ × *E. masquinongy* ♂, *E. reicherti* ♂ × *E. lucius* ♀ (9; 56–144), *E. reicherti* ♀ × *E. lucius* ♂ (9; 60–188), *E. reicherti* ♂ × *E. niger* ♀ (1; 135), and *E. reicherti* ♂ × *E. americanus vermiculatus* ♀ (5; 63–154). For comparison *E. reicherti* (9; 54–192) were produced from the same parental stock under the same conditions (see Fig. 1F). Sample specimens of all crosses made are in the reference collection, Department of Ichthyology and Herpetology, Royal Ontario Museum (ROM 29122–29139). For three of the crosses, *E. reicherti* ♀ × *E. niger* ♂, *E. reicherti* ♀ × *E. a. americanus* ♂, and *E. reicherti* ♀ × *E. a. vermiculatus* ♂, eggs failed to hatch. No specimen numbers for *E. reicherti* ♀ × *E. masquinongy* ♂ are listed above. This cross was successful and is known to have survived but is not described here because of a loss of integrity in the sample that resulted from a handling error. No female redfin pickerel, *E. a. americanus*, were available. The care given to the fertilization and rearing of the eggs of all the other combinations was uniform and meticulous.

For all characteristics, counts and measurements were derived from as many of the available specimens as would yield reliable results. Vertebral numbers were counted on radiographs.

The designation SL: SnL represents the proportion of standard length to snout length in millimetres. Values for dorsal and anal rays include all rudiments. Branchiostegal rays are given for ceratohyal plus epihyal on the right side followed by the same counts for the left side. Submandibular pores are given for the right side followed by the left side. Number of cardioid scales (notched scales) are given as A — those in the triangle between the pelvic fins, and B — those in the line between the origins of dorsal and anal fins. All lateral-line scales were counted, not just those to a point representing the end of standard length. The extent to which the cheeks and the opercles were covered by scales is given as tenths of the total area.

Since the hybrids all have *E. reicherti* as one parent, for simplicity we have used a hybrid designation in which all begin with the *E. reicherti* parent, rather than the taxonomic standard of giving the male parent first, or the genetic one with the female parent first.

Where the phenotypes of hybrids and parents are compared, the parental phenotypes used were the narrower ranges known for individuals from the same Pennsylvania sources, as listed by Crossman and Buss (1965), rather than the broader range of values for the total distribution of that species.

Since the Amur pike is relatively unknown in North America, we give the following brief description from Nikolsky (1956), Berg (1962), and specimens at ROM: anal rays 15–19, dorsal rays 17–22, branchiostegal rays (one side) usually 5 + 8 or 6 + 7, submandibular pores usually 5/5, rarely 6 on one side only, all lateral-line scales 130–165, cheek squamation up to 10/10, opercular squamation up to 5/10, vertebrae 60–65, length usually to 1 m, and weight to 16 kg in the USSR, but an Amur pike 114 cm TL was taken by an angler from Glendale Lake, Cambria Co., Pa. in 1976.

In general this species most closely resembles *E. lucius* in counts, measurements, and potential maximum size. The general coloration, however, is like that of the adults of *E. masquinongy* from the Great Lakes and St. Lawrence River; their pattern consists of dark markings on a lighter background, as opposed to the light markings on a dark background of *E. lucius*. In life, North American *E. reicherti* have the dorsal surface golden brown to green. The head and flanks are golden to pale brown and marked with brown to black, oval to round spots equal to, or slightly larger than, the pupil of the eye. The paired fins are golden to reddish brown and marked or unmarked; the dorsal, anal, and caudal fins are yellowish to reddish brown and marked with brown to black spots. Berg (1962) said that specimens up to 350 mm long have dark, narrow, oblique bands rather than spots. Bands were not seen on *E. reicherti* reared in Pennsylvania. Young of *E. reicherti* have no trace of the golden, middorsal stripe so characteristic of young *E. masquinongy*.

Unlike species of North American esocids there is apparently in the USSR no strong association of *E. reicherti* with heavily vegetated lakes and slowly moving rivers. The habitat is said to be among rocks in the central portion of moderately flowing rivers as well as lakes.

Results

Description of Hybrids (See Table 1)

Esox reicherti × *E. masquinongy* (Amur pike × muskellunge: Fig. 1A)

For these two parents the morphology of one reciprocal only, *E. r.* ♂ × *E. m.* ♀, is described. Both were attempted and successful, but a later problem cast doubt on the integrity of the sample of speci-

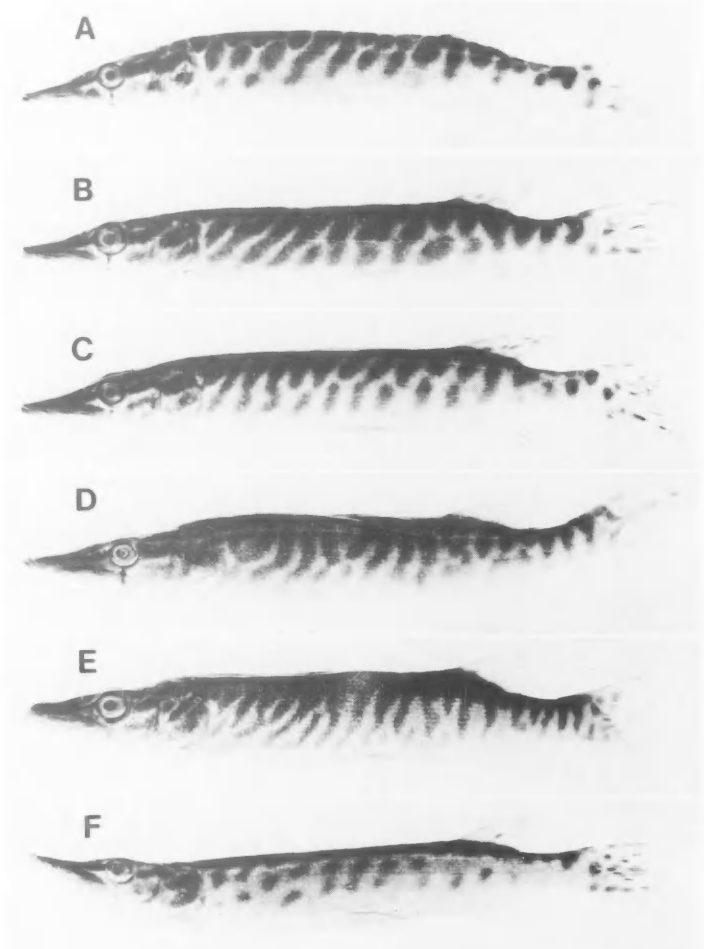

FIG. 1. A, *Esox reicherti* ♂ × *E. masquinongy* ♀ (148 mm TL); B, *E. reicherti* ♂ × *E. lucius* ♀ (133 mm TL); C, *E. reicherti* ♀ × *E. lucius* ♂ (188 mm TL); D, *E. reicherti* ♂ × *E. niger* ♀ (164 mm TL); E, *E. reicherti* ♂ × *E. a. vermiculatus* ♀ (154 mm TL); F, *E. reicherti* ♂ × *E. reicherti* ♀ (181 mm TL).

mens for *E. r.* ♀ × *E. m.* ♂. In pattern, the young of *E. r.* ♂ × *E. m.* ♀ closely resembled the young of *E. masquinongy*. None were spotted as the young *E. reicherti* were. The dark bars extending downward from the back were broad, almost vertical, and not as numerous nor like those described by Nikolsky (1956) for young *E. reicherti*. Snout length and anal rays were more like *E. reicherti*. Dorsal rays, submandibular pores, and branchiostegal rays were intermediate. Number of lateral-line scales was lower than either parent. Color pattern, head squamation, and number of vertebrae were like those of *E. masquinongy*. Cardioid scale numbers were similar in both parents and hybrid. The golden, middorsal stripe so characteristic of young *E. masquinongy* but not present in young *E. reicherti* did not appear in the hybrid.

In the cross involving eggs of *E. reicherti* and sperm of *E. masquinongy*, fertilization was poor, the hatch was <10%, and most fry died before absorption of the yolk had been completed. Approximately 20% of the eggs hatched when the sperm of *E. reicherti* and the eggs of *E. masquinongy* were crossed.

In the spring of 1975 a female hybrid *E. r.* × *E. l.* (gamete composition unknown) was backcrossed to

TABLE 1. A comparison of some of the characters of six hybrid combinations involving *E. reicherti*, and those for *E. reicherti*. See Materials and Methods for explanation of the expressions for characters and for number of specimens involved. SL:SnL is the proportion of standard length to snout length in millimetres. R = right; L = left.

Character	*E. r.* ♂ × *E. m.* ♀	*E. r.* ♂ × *E. l.* ♀	*E. r.* ♀ × *E. l.* ♂	*E. r.* ♂ × *E. n.* ♀	*E. r.* ♂ × *E. a. v.* ♀	*E. r.* ♂ × *E. r.* ♀
Total length (mm)						
Range	48–158	56–144	60–188	164	63–154	54–192
SL:SnL						
Range	5.22–7.44	4.38–7.87	6.25–7.94	6.75	6.10–10.25	5.63–7.41
Mean	6.1	6.7	6.9	—	7.5	6.7
Anal rays:						
Range	18–19	18–20	19–21	18	16–19	18–19
Mode	19	20	20	—	16 or 19	18
Dorsal rays:						
Range	20–22	21–22	21–24	20	18–21	20–21
Mode	22	22	23	—	20	20
Branchiostegal rays						
Range for two sides (R–L)	7+9–8+10	6+8–7+9	6+8–7+9	6+9	4+8–7+8	5+8–6+8
One side combinations	7+9, 8+9, 8+10, 9+9	6+8, 6+9, 7+7, 7+8, 7+9	6+8, 6+9	6+9	4+8, 5+8, 5+9, 6+8, 7+8	5+8, 5+9, 6+8
Submandibular pores						
Range for one side	5–7	4–5	4–6	5	4–5	4–5
Combinations R/L	5/5, 6/5, 6/6, 6/7	4/4, 5/5	5/4, 5/5, 6/5	5/5	5/4	4/4, 4/5, 5/5
All lateral-line scales	121–124	126–129	125–136	135	120–122	134–139
Head Scales as 10th of coverage						
Cheek	3	8–9	8–9	10	10	10
Operculum	5–6	5	5	6	8–10	4
Cardioid scales:						
A	0	0	0	0	0	0
B	0–1	0–1	1–4	0	2	1–2
Vertebrae	66	61–63	63	58	53–56	64–65

an *E. reicherti* male. The hatch was successful and 200 individuals were alive in December 1976.

Esox reicherti × *E. lucius* (Amur pike × northern pike: Fig. 1B, C)

In pattern, the young hybrids of *E. r.* ♂ × *E. l.* ♀ resembled *E. lucius* more than *E. reicherti*. The dark pigmentation on the flanks resembled the pale, flamelike, vertical bands characteristic of young *E. lucius*. The pale bands interrupt the general dark color, sometimes dividing it into large ovals of dark pigment but not into the precise and widely separated spots of *E. reicherti*. In *E. r.* ♀ × *E. l.* ♂ this separation is greater and the pattern approaches two rows of vertical oval spots with the position of the spots staggered. The result is closer to the pattern of some young *E. masquinongy* rather than that of either of the parents. The unpaired fins of both crosses bore small, round to oval, dark spots.

Values for characteristics of the two parental species were often very close and it is difficult to say whether the hybrids were like one parent or were intermediate. Snout length of the *E. r.* ♂ × *E. l.* ♀ cross seemed to be closer to that of *E. reicherti*, whereas that of the reciprocal was more variable, exceeding the range of both parents. The anal rays of *E. r.* ♀ × *E. l.* ♂ were closer to *E. lucius*, whereas that of the opposite cross spanned the range of both parents. The number of dorsal rays in *E. r.* ♀ × *E. l.* ♂ varied from intermediate to values for *E. lucius*, and those in *E. r.* ♂ × *E. l.* ♀ from intermediate to values for *E. reicherti*. Branchiostegal ray numbers in both crosses started in the highest values for *E. reicherti* and exceeded even the higher values of *E. lucius*. Submandibular pore number and head squamation were the same in parents and hybrids. Lateral-line scales of *E. r.* ♂ × *E. l.* ♀ were intermediate, but in *E. r.* ♀ × *E. l.* ♂ the numbers extended from the middle of the range for *E. lucius* to the upper limit of that for *E. reicherti*. *Esox r.* ♂ × *E.*

l. ♀ had lower values for cardioid scales than either parent, and *E. r.* ♀ × *E. l.* ♂ resembled *E. lucius*. The number of vertebrae in both crosses was intermediate to those of the parent species.

The cross *E. r.* ♀ × *E. l.* ♂ was more successful than the reciprocal. Fertilization in both crosses was good, percent hatch in *E. r.* ♀ × *E. l.* ♂ was 50–60, whereas in the reciprocal it was only approximately 20. However, individuals of both crosses survived and appeared to be normal.

In the spring of 1976 the backcross (*E. r.* × *E. l.*) × *E. r.* was attempted and the offspring survived as well as any of the hybrids and have been retained as a brood stock. Also in spring 1976, eggs from the hybrid *E. r.* × *E. l.* were fertilized with sperm from the same cross and survival was as good as that for successful F_1 hybrids; 186 progeny were liberated, unmarked, into Glendale Lake, Pa.

Esox reicherti × *E. niger* (Amur pike × chain pickerel: Fig. 1D)

For these two parents one cross only is represented, *E. r.* ♂ × *E. n.* ♀. The pattern for this hybrid was not similar to that of either parent nor to that of hybrids involving *E. niger* and other North American species. The flanks presented an impression of broad, dark, irregular bars with rounded ends, extending down from the dorsal surface. The paler spaces separating the bars almost equaled the bars in width. There was little coloring on unpaired or paired fins.

As in the cross with *E. lucius* the morphometric values for the parents involved are often close. In this cross, snout length, anal rays, dorsal rays, and submandibular pores fell within the ranges of both parents. Total number of branchiostegal rays (15) was similar to that common to both parents, but the rays were in an arrangement (6 + 9 − 6 + 9) known for *E. niger* and unknown in *E. reicherti*. Lateral-line scales, head squamation (fewer on operculum than *E. niger*), and number of cardioid scales were like those of the *E. reicherti* parent. The number of vertebrae was intermediate.

For the cross described, the fertilization rate was good, the percent hatch was 40–60, but 50% or more of the fry were crippled. The reciprocal, *E. r.* ♀ × *E. n.* ♂, was attempted but the eggs failed to hatch.

Esox reicherti × *E. americanus vermiculatus* (Amur pike × grass pickerel: Fig. 1E).

Only one of the two reciprocals of this cross is available, *E. r.* ♂ × *E. a. v.* ♀. The pattern of this hybrid rather closely resembled that of *E. l.* ♂ × *E. a. v.* ♀, consisting of vertical, dark, tigerlike stripes which extended down from the dorsal surface and were pointed at their ventral ends. The area of pale background between adjacent stripes was as great or greater than the width of a stripe. The unpaired fins were faintly marked with dark pigment.

In this hybrid the snout length varied from comparable to *E. reicherti*, to shorter than that of either parent. Numbers of anal rays, lateral-line scales, and vertebrae were intermediate to those of the parents. Numbers of dorsal rays in the hybrids varied from the lowest known for *E. a. vermiculatus* to the highest for *E. reicherti*. Some branchiostegal ray count combinations were higher than those of either parent but most were more like *E. reicherti* than *E. a. vermiculatus*. Two of the five individuals of this hybrid had five submandibular pores on each side; five is rare in *E. a. vermiculatus* but common in *E. reicherti*. Cheeks were completely scaled (as are those of both parents), but the opercula had more scales than *E. reicherti* and were closer to the condition in *E. a. vermiculatus*. The number of cardioid scales is similar in both parents and hybrids.

Fertilization appeared satisfactory in this cross: 40–60% of the eggs hatched, but 50% or more of the fry were crippled and survival was low. In the reciprocal, *E. r.* ♀ × *E. a. v.* ♂, the eggs failed to hatch.

Esox reicherti × *E. americanus americanus* (Amur pike × redfin pickerel)

No female redfin pickerel was available at the time the crosses were made. The reciprocal, *E. r.* ♀ × *E. a. a.* ♂, was attempted but none of the eggs hatched.

The grass pickerel and redfin pickerel differ only in certain scale and snout characteristics. Results using the males of the two forms were the same. It can then be supposed that had the *E. r.* ♂ × *E. a. a.* ♀ cross been made the results would have been similar to those for the *E. r.* ♂ × *E. a. v.* ♀ cross (i.e. 40–60% hatch, many cripples, low survival).

Discussion

None of the 10 reciprocal crosses represented here are even probable in nature. *Esox reicherti* and *E. lucius* occur in Asia but *E. reicherti* is restricted to the Amur River system, one of the limited number of Asian watersheds not inhabited by *E. lucius*. The other esocids are endemic to North America.

The very poor success in *E. r.* ♀ × *E. m.* ♂ and the failure to hatch in *E. r.* ♀ × *E. n.* ♂, *E. r.* ♀ × *E. a. a.* ♂, and *E. r.* ♀ × *E. a. v.* ♂ is considered to represent a case of incompatability rather than one of methodology. Considerable care was taken in the early stages of producing the hybrids and some of the hybrids showed relatively high survival under the same conditions. It is noteworthy that the failures all involve males of North American esocids.

Of their earlier study of hybrids of North American esocids Crossman and Buss (1965) said, "One of the surprises . . . . was the apparent low degree of interspecific sterility . . . . considering the relative

sizes at sexual maturity of the individuals involved." The surprise is even greater when there is survival of hybrids between the Amur pike and the pickerels, forms that not only differ greatly in potential maximum size but probably evolved in isolation on different continents.

The expected inverse relationship between survival of various crosses and relative size at sexual maturity of the parent species involved was apparent. Results were acceptable and good when Amur pike were crossed with muskellunge and northern pike respectively. These three species form an obvious subgenus of "pikes" (see opening paragraph). Results were much poorer when Amur pike were crossed with the "pickerels," a different subgenus of smaller species. The greatest number of truly intermediate values for morphometric characters in hybrids arose in those involving the "pikes." The number of characters that had values different from either parent, or values above and below those for both parents, was greater in hybrids involving "pickerels".

In all three cases involving eggs of *E. reicherti* and sperm of a "pickerel" no eggs hatched. This was not egg-effect, since eggs of the species with greater potential size were involved in each case. In all cases involving the male of a North American species the results were poor or a failure.

In the five successful crosses described, parental character resemblance (10 characters) in the hybrids was as follows: two were more like *E. reicherti* and three were more like the other parent. Of the three that resembled the other parent more than they did *E. reicherti*, two involved *E. lucius* and one *E. masquinongy*. The only character of *E. reicherti* that was carried through the hybrids, except for that involving *E. a. vermiculatus*, was dark spots on the unpaired fins. These spots are characteristic only of *E. reicherti* and *E. masquinongy* in nature. Otherwise in all the hybrids, pattern seemed more like the other parent involved. The number of vertebrae in four of the five hybrids was intermediate to that of the parents. Vertebral number is one of the best recognition characters.

The results indicate that there is little to be gained by holding up the appearance of this information on the hopes of successfully repeating the *E. r.* ♀ × *E. m.* ♂ and *E. r.* ♂ × *E. a. a.* ♀ crosses. In only one case (*E. r.* × *E. l.*) have hybrids been available over a period long enough to test fertility. A female of one of the *E. r.* × *E. l.* crosses appeared fertile and was backcrossed with a male Amur pike. This backcross yielded viable young. Davisson (1971) suggested that *E. r.* ♂ × *E. l.* ♀ hybrids produced F_1 young fertile in both sexes.

These results seem to amplify the suggestions that arose from the earlier study (Crossman and Buss 1965), that complete genetic incompatibility does not occur in the family. Fertile, F_1 hybrids can be developed not only within those species of this family that occur, and probably evolved, in the Nearctic (*E. masquinongy*, *E. niger*, and *E. americanus*) but also within the two species (*E. reicherti* and *E. lucius*) that probably evolved in the Palaearctic. Other barriers, geographical and behavioral, must help maintain the genetic integrity of the species, since the frequency of hybrids is low even in areas in which two of the species overlap.

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Structure of Pelagic Food Chain and Relationship Between Plankton and Fish Production[1]

R. W. SHELDON, W. H. SUTCLIFFE JR., AND M. A. PARANJAPE

Department of Fisheries and the Environment, Fisheries and Marine Service, Marine Ecology Laboratory, Bedford Institute of Oceanography, Dartmouth, N.S. B2Y 4A2

SHELDON, R. W., W. H. SUTCLIFFE JR., AND M. A. PARANJAPE. 1977. Structure of pelagic food chain and relationship between plankton and fish production. J. Fish. Res. Board Can. 34: 2344–2353.

Further observations on the standing stocks of pelagic organisms confirm the occurrence of approximately equal biomass over logarithmically equal size ranges. A simple theoretical framework is developed that shows that the structural elements of the pelagic ecosystem can be described in terms of the sizes of predator and prey and of the efficiencies of their interactions. In practice this means that if the standing stock at any size range is known, the standing stock at any other size can be estimated, and if the growth rate at this size is known, the production can be estimated. The theory is tested on three fisheries. For the Gulf of Maine and the North Sea, phytoplankton production is estimated from fishery production. For the area off Peru the fishery production is estimated from the plankton production.

Key words: pelagic ecosystem, predator–prey relationships, plankton production, marine fisheries, Peru, North Sea, Gulf of Maine

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Si l'on ordonne les organismes pélagiques selon leur taille sur une échelle logarithmique, on trouve que la quantité de matière vivante est égale pour chaque taille. C'est-à-dire que la concentration (milligrammes par litre) soit de plancton, de poissons ou d'organismes intermédiaires est la même dans chaque intervalle logarithmique. Nous avons formulé une description mathématique simple qui démontre que l'on peut décrire la structure de la chaîne alimentaire pélagique en ne considérant que la taille des prédateurs et de leurs proies, et les rapports existant entre les deux. En utilisant notre formulation on peut estimer la production d'une pêcherie en mesurant par exemple, la quantité de plancton et le taux de croissance des poissons. Nous avons appliqué la théorie à trois pêcheries. Dans le cas du golfe du Maine et de la mer du Nord, nous avons estimé la production du plancton par rapport à la production des poissons. Pour la région côtière du Pérou nous avons estimé la production des anchois par rapport à la production du plancton.

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OCEANIC pelagic environments are remote from normal research facilities. They are difficult to get to and even more difficult to stay in, and this makes the pelagic ecosystem somewhat less than an ideal choice for study. This is further compounded by the fact that, at least in the subtropics, the ecosystem structure seems to be incredibly complex. The number of species is large and their apparent web of interactions is, at first sight, bewildering. However, there are certain features of the pelagic environment that are appealingly simple. Climatic and ecological stability are obvious examples. The basic trophic structure also seems to be simple (Sheldon et al. 1972; Kerr 1974) even though the details are undoubtedly complex. In this study we extend the simplified view of the pelagic food chain, based essentially on particle size spectra, and show that by considering the interactions of organisms relative to their size we can arrive at a plausible structure for the pelagic food chain; from this we derive reasonable estimates of plankton and fish production.

[1]Bedford Institute of Oceanography Contribution.

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Structure of Pelagic Food Chain

PRACTICAL CONSIDERATIONS

We can characterize the trophic structure of pelagic ecosystems by considering three factors (Sheldon et al. 1973). The first concerns the nature of the primary production. With some notable excep-

tions (*Sargassum* for instance), most of the primary organic production in the sea is by single-celled plants. The second concerns the nature of the first trophic link. Most herbivores are small, but they are usually larger than the plants. The third concerns the relationships of the higher trophic levels. In the sea, organisms at higher trophic levels tend to be larger than those at lower trophic levels. It is, in fact, virtually a biological law that among the plankton and the nekton a predator is larger than its prey (Marshall 1971, p. 6), although this is not so generally true of the benthos. It is easy to see why this should be. An aquatic animal lives in a medium 800 times denser than air and efficient movement can only be achieved by streamlining (Marshall 1971, p. 23). Appendages that could be used for grasping a large food object are inconvenient and are not commonly developed. A predator must take its prey by swallowing it and must therefore be larger than the prey.

The structural limits imposed by a truly aquatic mode of life allow relatively little variation in form, and in contrast to, say, terrestrial animals, most pelagic fish have a similar shape. As the shapes are similar one would expect that the ratio of size of predator and prey (at least at the higher trophic levels) would also be fairly constant.

In a steady state system a predator can only consume the growth of its prey population. It must not make permanent inroads into the basic stock. In other words, it must live on the interest and not touch the capital. As the growth rate of a population will vary with the average size of the organisms (Fenchel 1974), the stock of prey required to provide a predator with a given amount of food will also vary with the size of the prey. A small stock of small prey could provide the same production as a large stock of large prey. In terrestrial systems a predator of any particular size could, theoretically, have a wide choice of prey size. A 25-kg predator could, for instance, live on ants, rabbits, or antelopes (depending on its own evolutionary adaptations) and the standing stock of its prey would vary accordingly. But in the sea there are fewer options available. Whatever its adaptation or mode of life a predator tends not to live on prey that is very much larger or smaller than about 7% of its own length (D. Ware personal communication). Those that do, e.g. lampreys, tend to follow unusual and specialized adaptations and are beyond the scope of our discussion. One would expect, therefore, that as the size ratio of predator and prey does not vary greatly, then the ratio of the standing stocks will also be similar.

Some observations have been made that suggest that standing stock does not vary much with size (Sheldon et al. 1972), and recent theoretical studies indicate that given the observed predator to prey body size ratios, the ratios of standing stocks may approximate to unity (Kerr 1974). As the predator and prey populations are likely to each have the same logarithmic variation in size, it follows that standing stocks over logarithmically equal size intervals will be similar (see Sheldon et al. 1972 and Fig. 1).

The original concept of roughly equal standing stocks within equal logarithmic size intervals was developed mainly from observations in the size range 1–100 μm, with a few observations at sizes around 1 mm (Sheldon et al. 1972). We have now made further observations in the Sargasso Sea that extend over a size range from 0.5 μm to about 2 cm (Fig. 1). This covers more than 4 orders of magnitude of linear dimensions. As the complete food chain from primary producer to terminal predator extends over <6 orders of magnitude, the observations cover more than two thirds of the food chain in terms of size and also account for two thirds of the total biomass.

Particle size distributions shown in Fig. 1 were derived from two sets of samples. Small particles (0.5–80 μm) were collected with a float and bottle sampler (Sheldon et al. 1973) at a depth of 4 m, and the particle size distributions were analyzed with a Coulter counter (Sheldon and Parsons 1967a). The adenosine triphosphate (ATP) content of prescreened (160 μm) samples was determined by the method of Holm-Hansen and Booth (1966). Large particles (zooplankton >250 μm) were collected

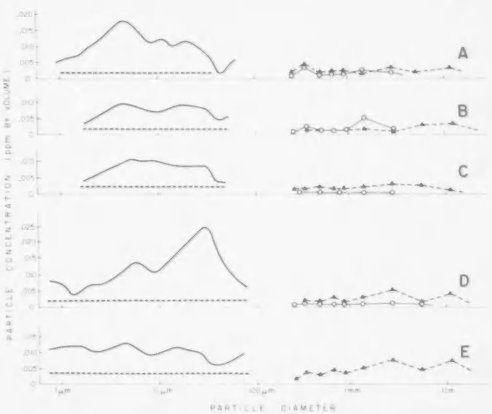

FIG. 1. Pelagic standing stocks (concentration per size grade) in the surface waters of the Sargasso Sea. O——O, Zooplankton concentrations, day samples; Δ——Δ, zooplankton concentrations, night samples; ———, total concentration of small particles; ------, average concentration of small living particles estimated from ATP measurements. A, 25°54′ N, 62°45′ W, February 6, 1975; B, 25°56′ N, 62°45′ W, February 7, 1975; C, 25°33′ N, 62°40′ W, February 8, 1975; D, 32°51′ N, 62°41′ W, February 11, 1975; E, 32°45′ N, 62°32′ W, February 13, 1975.

with a conventional ($\frac{1}{4}$ m diam) metered net towed across the wind at 5 m depth. Size distribution of the zooplankton was determined by wet sieving the fresh material immediately after sampling. Sieves of various sizes were used, depending on the sample, so that measurable amounts of zooplankton were retained on each. Results have been recast in Fig. 1 to show the volume of material in a standard size grade. Each grade covers a relative diameter range of 2^1. This scale has been fairly widely used in studies of marine particle and plankton distributions (e.g. Sheldon and Parsons 1967b; LeBrasseur et al. 1969; Parsons 1969; Sheldon et al. 1972; Poulet 1974; Conover 1977; Sheldon 1977). It is similar to the standard scales used for granulometric analysis (Krumbein and Pettijohn 1938; Sheldon 1969).

It is easy to see whether or not the individuals in a freshly taken zooplankton sample are alive, and the right-hand side of Fig. 1 represents the amount of living organisms (per standard size grade) in the size range from about 250 μm to 2 cm. However, the situation with small particles is less simple. We were able to see living organisms and nonliving particles in filter concentrates but we did not know in what proportion these occurred in the original samples. For an estimate of living material we had to depend on measurements of ATP content of the total sample. Solid curves on the left-hand side of Fig. 1 represent the particle concentration per size grade, as measured, and the broken lines represent the average concentration of living material per size grade as estimated from the total ATP values.

Figure 1 shows that the hypothesis tentatively advanced by Sheldon et al. (1972) — that roughly equal standing stocks occur over logarithmically equal size intervals — is confirmed within the limits of accuracy of our observational techniques. In the next section we develop a structure for the pelagic food chain based on the assumption that the logarithmic distribution of biomass is constant and independent of size. We then extend this to consider the range of biomass distribution that could reasonably occur.

Theoretical Considerations

If we define production as the formation of living material, then the relationship between the production of a predator and its prey can be expressed as

$$P_c = P_p \cdot G_e \cdot C_e \tag{1}$$

where P_c is the amount of predator tissue formed, P_p is the amount of prey tissue formed, G_e is the growth efficiency (defined as the quantity of predator tissue formed relative to the amount of prey ingested), and C_e is the predation efficiency, i.e. the proportion of the prey production taken by the predator. Equation (1) is not particularly useful because none of the quantities can be measured easily, but we can substitute into the equation variables that we can measure, and from these we can estimate those variables that we cannot measure. In a steady state system, natural populations will tend to grow exponentially and this growth will be removed as fast as it is formed. Under such conditions the production is expressed simply as $P = r\,S$, where r is the instantaneous growth rate and S is the standing stock. In any one population the average growth rate is constant, but it will vary between populations depending on the average size of the organisms (Fenchel 1974).

We can therefore write (1) as

$$r_c S_c = r_p S_p \cdot G_e \cdot C_e \tag{2}$$

where r_c, S_c, and r_p, S_p are the instantaneous growth rates and standing stocks of predator and prey, respectively. Rewriting (2):

$$r_c/r_p = S_p/S_c \cdot G_e \cdot C_e \tag{3}$$

If S_p/S_c is approximately unity, it follows that

$$r_c/r_p = G_e \cdot C_e \tag{4}$$

There is a definite relationship between growth rate and body size that is simply a variant of the well known "metabolic law." This can be expressed as $r = aW^n$, where W is the body weight and a and n are constants. Fenchel (1974) considers n to have a value of around -0.275. We have also calculated n (but using only data for plankton and fish) and arrive at the expression $r = aW^{-0.24}$, or $r = bD^{-0.72}$, where D is the equivalent spherical diameter and a and b are constants that depend on the environmental temperature. The ratio of growth rates can therefore be expressed as a ratio of sizes.

$$r_c/r_p = (D_c/D_p)^{-0.72} = G_e \cdot C_e \tag{5}$$

For the purposes of this study, equation (5) describes the size structure of a pelagic food chain with equal standing stocks of predator and prey.

This size structure is not subject to much variation. Copepods will take prey over a wide range of size (Conover 1977) with an average ratio in the range 20–30 (Sheldon et al. 1972; Poulet 1974), and a ratio of around 100 could be reached by certain oceanic pteropods (Gilmer 1972) or tunicates (Alldredge 1972) that feed directly on nanoplankton. But for many pelagic organisms the size ratio of predator to prey tends to cluster around a value of 14 (Fig. 2). If we substitute this average value in equation (5) we find that $G_e \cdot C_e = 0.15$; that is, if a predator takes all the prey production, then it must have a growth efficiency of 15%. If only 80% of the prey production is taken, then the growth efficiency must be 19%. If larger prey are taken (i.e. $D_c/D_p < 14$) then the growth efficiency must increase in spite of the fact that all the prey production is taken. This might be difficult for a predator to achieve. In

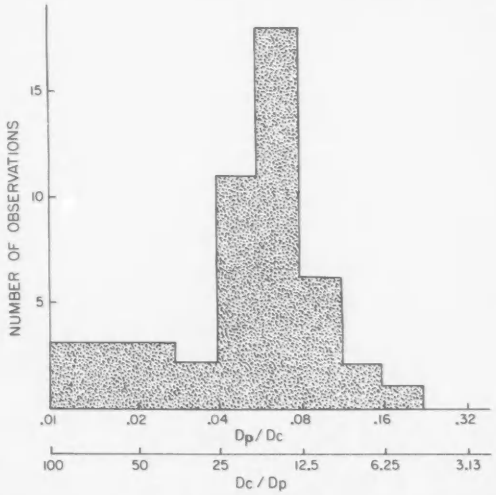

FIG. 2. Histogram of the ratio of the size of various pelagic predators relative to their prey. D_c = equivalent spherical diameter of predator and D_p that of prey. Data sources as follows: copepods: Poulet (1974), Parsons et al. (1969), Parsons and LeBrasseur (1970); herring: Blaxter (1973) Lebour (1924) Guryeva (1973); young salmon: Parsons and LeBrasseur (1970); redfish larvae, Cod larvae: Bainbridge and McKay (1968); haddock larvae, Pollack larvae: Marak (1960).

evolutionary terms it might be easier for a predator to adapt to smaller prey. With D_c/D_p at 20, equation (5) would be $G_e \cdot C_e = 0.11$. This means that with 15% growth efficiency a predator would only have to take 73% of the prey production. However, a trend towards utilizing smaller prey could be self-defeating, as small prey may be difficult to catch in quantity. This difficulty would be relieved somewhat if the prey occurred in patches.

The structure of the pelagic food web might not be as restrictive as equation (5) indicates. In equation (3) we eliminated S_p/S_c by assuming that it was unity. While this is probably true on average, the ratio varies with the particular predator–prey relationship considered. In Fig. 3 we have rearranged equation (3) and plotted the relationship between the ratio of the standing stocks and the ratio of the sizes of predator and prey. The three lines are for different values of $G_e \cdot C_e$. If we assume that C_e is unity, i.e. all the prey production is taken by the predator, then the lines represent the relationships for growth efficiencies of 10, 15, and 20%. If we take an average predator to prey size ratio of 14 (Fig. 2) and project it to the average growth efficiency of 15%, the corresponding ratio of standing stocks is close to 1. This we assumed in development of equation (5). If we consider a range of predator to prey ratios from 5 to 25 (Fig. 2) and consider a range of growth efficiencies from 10 to 20%, then the standing stocks could vary from about 0.3 to 2.0. The hatched area represents the range of structure that could reasonably occur, although the range in any one system would probably be less than this.

Relationship Between Plankton and Fish Production

The trophic structure we have postulated describes the interaction of predator and prey, and to relate fish and plankton production one would have to know the number of predator–prey links involved. However, we can eliminate the consideration of trophic levels and relate plankton and fish directly if we make certain reasonable assumptions.

1) Predator efficiency is 100%. According to the review by Steele (1974) the plant production in the sea is rapidly used by the herbivores, and there is little reason to doubt that a similar situation exists at higher trophic levels. However, it is very difficult to demonstrate unequivocally that 100% predation is the rule. McAllister (1969) gives data for monthly mean standing stocks of phytoplankton and zooplankton for 6 yr at Ocean Station P (50° N 145° W) in the North Pacific (McAllister 1969, fig. 3). We recast his data and obtained the following relationship (in terms of milligrams carbon per square metre):

$$\text{Zooplankton} = 1.5\ (\pm 0.3)\ \text{Phytoplankton} - 270\ (\pm 180)$$

The ratio of 1.5 would, according to McAllister (1972, fig. 1), indicate a transfer efficiency (equivalent to growth efficiency if predation = 100%) of 15%. If the size ratio of the zooplankton to the phytoplankton averaged around 30 (Sheldon et al. 1972, fig. 13), we would also predict a growth effi-

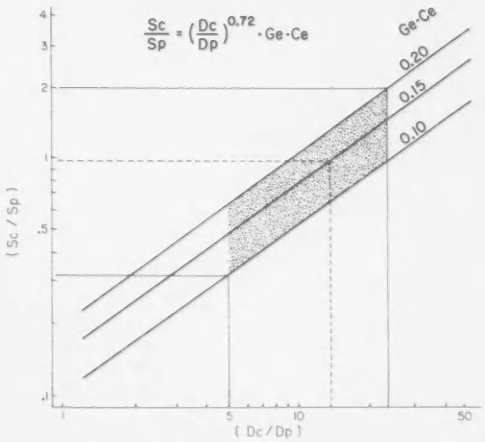

FIG. 3. Relationship between standing stock, size, and growth efficiency of predator and prey (for further explanation see text).

ciency of 15% (see Fig. 3), providing that the predation was 100%.

2) Standing stocks are similar at all sizes. This is not a particularly new concept. Harvey (1950) showed that in the English Channel the standing stocks at different trophic levels were roughly similar, and Odum (1971, fig. 3–6), working from energetic considerations, has shown very clearly why marine and terrestrial standing stock patterns are fundamentally different and why marine standing stocks are likely to be roughly constant and independent of the size of the organisms concerned. It follows from this that the production at any trophic level depends only on the growth rate, and thus the size of the organisms concerned (equation 5).

3) Apart from seasonal variation, most ecological systems are in a steady state. Many studies have been made since the idea of the "balance of nature" was first formally proposed (Darwin 1859), and it is now considered to be self-evident that in the long term, ecological systems must be in a steady state.

If these assumptions are accepted, then the production at any trophic level can be calculated if the standing stock or production at one trophic level is known. To illustrate this we consider two examples. In the first we start with a known fish production and estimate the plankton production needed for this, and in the second we start with a known plankton production and estimate the maximum fish production that could occur.

Gulf of Maine Fishery and the Plankton Production Supporting It

The production of individual fisheries in the Gulf of Maine varies greatly from year to year, but until the large foreign fleets appeared in the 1960s the total catch for all fisheries had remained more or less constant for many years (Sutcliffe et al. 1977). It seems that (during 1940–59) as the production of one fishery declined fishermen switched their efforts to another, and in this way they extracted a constant yield from the environment.

To estimate the plankton production needed to support the fish we assume initially that the total fish landings represent the total fish production. This is incorrect, but it is used simply to provide a base for calculation and will subsequently be modified. We further assume that the average size of the fish is similar to that of a small Atlantic cod (*Gadus morhua*) and that the relative size range of the fish is about half that of the phytoplankton; i.e. the smallest and largest fish differ by a factor of 4 in linear dimensions, while the phytoplankton differ by a factor of 10. Total standing stock of the fish would then be about 70% of the standing stock of the phytoplankton (Fig. 4). If these assumptions are accepted, it is only necessary to know the average growth rates of the plankton and fish (plus the total fish catch) for an estimate of annual phytoplankton production to be made.

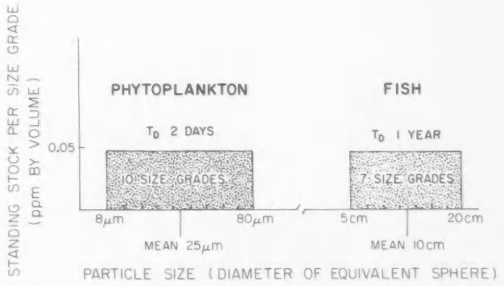

FIG. 4. Relationship between size, standing stock, and growth rate for phytoplankton and fish in the Gulf of Maine. (Note that for sizes to be compared a common scale is used — the diameter of an equivalent sphere. Actual fish lengths would be 3–4 times greater, depending on shape.)

In the Gulf of Maine, fish the size of cod could possibly double their standing stock in about a year (Sheldon et al. 1972, fig. 13). Annual catch should therefore equal the standing stock, which would be the same as the annual production, bearing in mind the assumption made above. As the area of the Gulf of Maine (to the edge of the continental shelf) is about 1.4×10^{11} m^2 and the average annual fish catch is about 4.2×10^{11} g (Fig. 6), the average annual fish production works out to be 3.0 g·m^{-2}·yr^{-1} (wet wt).

Average growth rate of the phytoplankton in the Gulf of Maine is not easy to estimate because there is much seasonal variation. The maximum rates that have been recorded elsewhere indicate a possible minimum doubling time for the Gulf of Maine phytoplankton of about a day (Cushing 1959; Eppley 1972; Sheldon et al. 1972), but the average doubling time is probably nearer to 2 days (Eppley and Strickland 1968).

Production rate of the phytoplankton should therefore be about 180 times greater than production rate of the fish. After taking into consideration the differences in standing stock, total phytoplankton production should work out to about 260 times the total fish production. This would be about 780 g·m^{-2}·yr^{-1} (wet wt). In terms of organic carbon this represents about 45 g C·m^{-2}·yr^{-1} (C/V ratio from Mullin et al. 1966). The available estimates for primary production on the northeastern seaboard of North America would lead one to expect a production in the Gulf of Maine of about 100–200 g C·m^{-2}·yr^{-1}. Our estimate is therefore rather more than a factor of 2 too low.

The reason for this lies with our original assumption that fish catch represented all fish production. The relationship between fish landed from a fishery and actual fish production is not completely understood, but reasonable limits can be set. Dickie (1972)

has suggested that for the maximum sustained yield the catch can be no more than about half the production. This would give us a minimum estimate of plankton production of 90 g $C \cdot m^{-2} \cdot yr^{-1}$. On the other hand, Edwards (1968) has estimated that the annual fish catch in the Gulf of Maine represents about one quarter of the standing stock. This would give a possible maximum estimate for phytoplankton production of 180 g $C \cdot m^{-2} \cdot yr^{-1}$. We should also consider that fish production will occur in species not taken commercially, but there would have to be a significant production by noncommercial fish of the same size as the commercial species for this to affect our estimates.

An obvious criticism of these estimates is that because we knew the answers and because we had to make certain assumptions, it was not too difficult to arrange the assumptions to give the correct answers. We can partially satisfy such criticism by applying exactly the same assumptions we used for the Gulf of Maine to the fisheries of the North Sea. Steele (1974) gives data on the North Sea fish catch that indicate that between 1909 and about 1955 the total fish landings remained fairly constant at about 1×10^6 $t \cdot yr^{-1}$. Using the data given by Steele (1974) and using exactly the same assumptions as we have outlined above for the Gulf of Maine, we obtain initial estimates of fish production of 2 g $\cdot m^{-2} \cdot yr^{-1}$, and plankton production of around 500 g $\cdot m^{-2} yr^{-1}$ (wet wt), which is equivalent to about 30 g $C \cdot m^{-2} \cdot yr^{-1}$. If, as in the Gulf of Maine, we assume that steady state landings represent between a quarter and a half of the fish production, we would estimate North Sea phytoplankton production to lie between 60 and 120 g $C \cdot m^{-2} \cdot yr^{-1}$. Primary production in the North Sea is around 70–90 g $C \cdot m^{-2} \cdot yr^{-1}$. (Steele 1974).

We have related the estimates of fish and plankton production according to our ideas on the structure of pelagic food chains in spite of the fact that the fisheries in the Gulf of Maine and the North Sea are pelagic and demersal. However, providing that we consider only the primary and terminal producers our estimates are valid.

A proportion of the phytoplankton production will settle from the surface waters (Stephens et al. 1967; Hargrave 1975) and therefore will cease to be part of the pelagic system. But this production is consumed by benthic organisms that are themselves consumed by demersal fish. In this way all the phytoplankton production is ultimately funneled by either the pelagic or demersal route into fish production. For our purposes this food chain can be considered "pelagic." We could not have made similar estimates to relate phytoplankton production to zooplankton production, for to do this we would have had to have known the proportion of the phytoplankton production that remained in the surface waters and was thus available to the zooplankton.

Plankton Standing Stock off Peru and the Anchoveta Fishery Supported by It

It is little more than an interesting academic exercise to use data from a heavily exploited fishery, collected over many years, simply to estimate phytoplankton production. It is much easier to measure plankton production directly. However, the reverse process is possible. If the phytoplankton production or standing stock is known, the fish production can be estimated.

The anchoveta fishery of Peru differs from the fisheries of the Gulf of Maine and the North Sea in that it is truly pelagic. High levels of utilization, particularly of primary production, are typical of pelagic food chains (Greze 1970), and very little settles out (Riley 1970; Ryther et al. 1971). With such a system we are not limited to considering only primary producers and terminal predators. We can estimate the standing stock or production of any trophic level from a knowledge of any other. In the following treatment we estimate the anchoveta production from a knowledge of phytoplankton and zooplankton standing stocks and anchoveta growth rate.

Phytoplankton standing stocks of the Peruvian region are not well known but primary production has been measured. Strickland et al. (1969) found that production varied from 0.25 to 4.1 g $C \cdot m^{-2} \cdot day^{-1}$, with most of the observations being greater than 1 g $C \cdot m^{-2} \cdot day^{-1}$. Barber et al. (1971) measured production of 1.1 and 3.5 g $C \cdot m^{-2} \cdot day^{-1}$ at two stations, and Cushing (1971) considered a range of between 1 and 4 g $C \cdot m^{-2} \cdot day^{-1}$ to be typical of an upwelling area. Ryther et al. (1971) found that production varied from about 1 to 11 g $C \cdot m^{-2} \cdot day^{-1}$, but was typically around 5 g $C \cdot m^{-2} \cdot day^{-1}$. The average situation given by Cowles et al. (1977) shows a band of high production (5 g $C \cdot m^{-2} \cdot day^{-1}$) within 95 km of the coast and an area of lower production (in the range 1–5 g $C \cdot m^{-2} \cdot day^{-1}$) extending about 300 km offshore. A production in the range 2–4 g $C \cdot m^{-2} \cdot day^{-1}$ would indicate a standing stock of about 2–4 g $C \cdot m^{-2}$, as the doubling time of the phytoplankton is about a day (Strickland et al. 1969). This would be equivalent to about 35–70 g $\cdot m^{-2}$ wet wt (assuming an average size of 25 μm); but to estimate the standing stock per size grade we have to know the size range of the phytoplankton. In the absence of better data we assume as before that they occupy 10 grades. The phytoplankton standing stock will therefore be in the range 3.5–7.0 g $\cdot m^{-2}$ per size grade.

According to Reid (1962) the average zooplankton standing stocks off Peru vary from 30 to 60 g $\cdot m^{-2}$. Net-caught zooplankton typically occupy 7 size grades (Sheldon and Paranjape unpublished data). Average concentration would therefore fall in the range 4–8 g $\cdot m^{-2}$ per size grade. Using data of Pavlov

(1968) for a similar upwelling region off West Africa we obtain a zooplankton standing stock of 5 $g \cdot m^{-2}$ per size grade.

We now have to consider how the level of anchoveta standing stock relates to that of phytoplankton and zooplankton. In the examples for the Gulf of Maine and the North Sea we were dealing with broad averages. We considered all kinds of catchable fish, pelagic and demersal, and the production by these would depend on many kinds of interactions at all stages of the food chain. We therefore assume for these cases that the average conditions indicated in Fig. 4 would apply and that plankton and fish standing stocks would be similar.

The food chain leading to the anchoveta is much simpler. It consists ideally of diatoms, copepods, and anchoveta, but some of the anchoveta bypass the copepods and take diatoms as part of their diet (deMendiola (1971). As we know roughly the relative sizes of the three groups making up the food chain, we can attempt to demonstrate the relationships between the standing stocks of the anchoveta and those of the smaller organisms of the food chain.

In the first link of the food chain the copepod–diatom size ratio is likely to be around 30 (Seldon et al. 1972; Poulet 1974). We would expect from this (see Fig. 3) that the standing stock of the copepods would be 1.5 times that of the diatoms (Fig. 5). On the other hand, the anchoveta–copepod size ratio is around 15 and we would expect the standing stocks to be equal; but as some anchoveta feed on diatoms this should lead to a relative increase in the anchoveta standing stock levels. We assume therefore that the anchoveta stocks are similar to the upper limit of the zooplankton stocks (Fig. 5) and that the anchoveta has an average standing stock of 8 $g \cdot m^{-2}$ per size grade. According to the growth data of Jordan (1974), the smallest and largest individuals (in the fishery) will not differ by more than a factor of 8 (by wt) and will occupy 3 size grades. The total standing stock of anchoveta in the fishery will therefore be 24 $g \cdot m^{-2}$.

The area of upwelling off Peru is about 5×10^{11} m^2

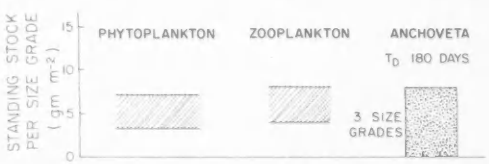

FIG. 5. Relationship of standing stocks of phytoplankton, zooplankton, and anchoveta off Peru. Hatched areas show the calculated range of phytoplankton standing stock and the observed range of zooplankton standing stock. (For further explanation see text.) Note that only the standing stock per size grade of the plankton need be known (not their size range) and that only the size range and growth rate of the anchoveta need be known (not their absolute size).

(Longhurst 1971), and according to FAO data (Anon. 1972), anchoveta are found (up to 300 km offshore) over a similar area. But according to Idyll (1973), the anchoveta fishery extends only 100 km offshore in an area corresponding to the zone of high average primary production defined by Cowles et al. (1977). We have taken Idyll's distribution as probably being the most correct representation and arrive at 2.4×10^{11} m^2 for the area of the fishery. Total anchoveta standing stock should therefore be about 60×10^{11} g.

From the growth pattern of anchoveta (Jordan 1974) one can estimate that a population growing exponentially would have an instantaneous growth rate of about 0.00385 $\cdot day^{-1}$. Such a population would double its biomass in about 6 mo. Yearly production will depend on how often the growth is removed from the population. If a day's growth is removed each day, then the yearly production would be 85×10^{11} g. If, on the other hand, the population was allowed to double before the growth was removed, then the production for the year would simply be twice the standing stock, or 120×10^{11} g. Clearly neither of these two extremes is probable and the true yearly production (available to a fishery) is probably somewhere between the two estimates. An estimate of annual production of, say, 100×10^{11} g would seem reasonable. Actual landed catch ranged from 85 to 123×10^{11} $g \cdot yr^{-1}$ between 1966 and 1971. (Fig. 6)

Discussion

When predictions from theory agree reasonably well with observation it does not necessarily mean that the two are perfectly in tune. The question of accuracy has to be considered, and this is not a particularly easy question to answer. However, it is possible to give some indication of the accuracy of our predictions.

Fisheries of the Gulf of Maine and the North Sea are the easiest to deal with. In these areas fish catch and area of the fishery are well documented. The food web is complex, which means that in spite of variations in predator and prey interactions many of the variations of standing stock are smoothed out before the end of the food chain is reached. The movement of fishing effort from one species to another also smooths out variations in total production. This means the average situation shown in Fig. 3 tends to apply, and it is possible therefore to predict fish standing stocks fairly accurately from average phytoplankton standing stocks.

For a sustained fish yield in a temperate region the annual fish catch should be between one quarter and one half of the standing stock. (Edwards 1968; Dickie 1972). Growth rate of the fish is such that the doubling time (T_d) of many commercial species is about a year (Sheldon et al. 1972). In this case fish catch would also be between one quarter and one

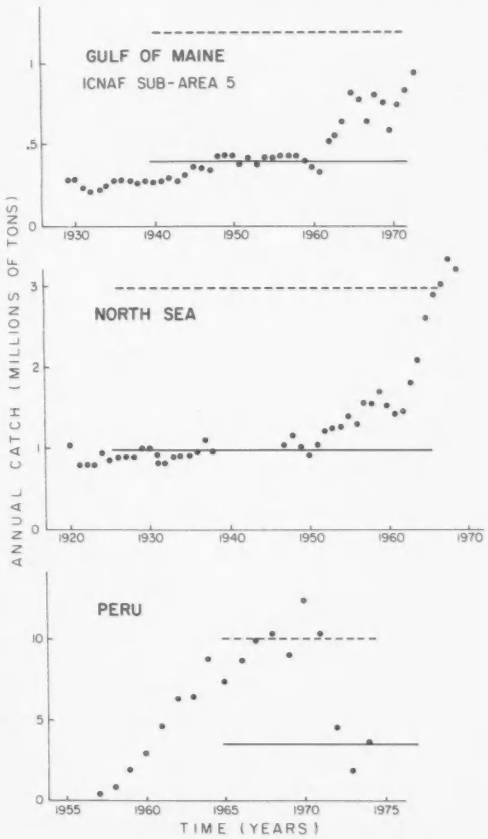

FIG. 6. Annual landings of all fish (pelagic and demersal) from the Gulf of Maine and the North Sea and of anchoveta from Peru. ———, Predicted fish catch if one third of the natural fish production is taken; ------, predicted fish catch if all the natural fish production is taken.

half of fish production. In Fig. 6 we show the fishery production we would predict (from considerations of phytoplankton standing stocks) if one third of the natural production were taken by the fisheries. This fits very well for those times when the same amount of fish was taken year after year; and this is a good indication that a sustainable yield was exploited. Whether or not this was the maximum sustained yield is, of course, open to question. If the maximum sustained yield is about one half of the natural fish production (Dickie 1972); we would predict that the Gulf of Maine should produce 0.6×10^6 t·yr^{-1} and the North Sea 1.5×10^6 t·yr^{-1}. Present production in the Gulf of Maine is at about this level but the level for the North Sea was exceeded in 1962.

While the food web of the Peru system is simpler than those of the North Sea and the Gulf of Maine, prediction is more difficult. This occurs because with fewer links and interactions there is less chance of stabilization by the averaging effect of many variables. However, the predicted fishery yield, on the assumption that one third of the natural fish production is taken by the fishery, gives estimates that are not greatly different from the recent catches. But there is considerable doubt as to whether the present catch levels represent a stabilization of the fishery after the boom years of the late 1960s or whether it is simply a reaction to the *El Niño* phenomenon.

In the case of the anchoveta the maximum sustained yield is not easy to define. We are not dealing here with a relatively slow-growing terminal predator; rather more than one half of the natural fish production could possibly be taken by a fishery without unbalancing the system. After the 1965 *El Niño* the fishery increased but the seabird population did not; yet after the 1957 *El Niño* the seabird population increased rapidly (Schaefer 1970; Idyll 1973). At that time there was no significant fishery in the area. From this we could conclude that the "natural" and fishing mortalities are related. As fish catch increases the amount available to the seabirds decreases. In recent years the birds are believed to have taken about 25% and the fishery 75% of the anchoveta production (Idyll 1973). If anchoveta mortality were due only to birds or fishing, then we could say that the maximum sustainable yield, predicted from zooplankton standing stocks, would be around 7.5×10^6 t·yr^{-1}. This is very close to the estimate of 8×10^6 t·yr^{-1} (quoted by Longhurst 1971), which was derived from catch effort data.

The major uncertainty in predicting the Peru landings lies in the estimate of the area of the fishery. In the North Sea and the Gulf of Maine good records are kept of where the fishing boats operate and hence the area of the fishery is known with reasonable accuracy. This is not so off Peru. Fish landings are well documented but the area from which the fish are taken is not. Therefore, even if prediction of fish production per unit area were perfectly accurate, the prediction of the total fish production would only be as accurate as the estimate of the total area of the fishery.

The advantage, as we see it, of using the food chain model we have developed to attempt to predict fish production is that it can be done in an area of unknown potential before a commercial fishery is started. In contrast, the conventional methods of assessing fish production — stock assessment or catch-per-unit-effort data — require that a fishery, or at least biological sampling that approximates to a fishery, be in operation at the time that the estimates are made.

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Habrobaenus hudsoni n.gen., n.sp. and the Immatures of *Baeoctenus bicolor* Sæther (Diptera: Chironomidae)

OLE A. SÆTHER

Department of Fisheries and the Environment, Fisheries and Marine Service, Freshwater Institute, Winnipeg, Man. R3T 2N6[1]

SÆTHER, O. A. 1977. *Habrobaenus hudsoni* n.gen., n.sp. and the immatures of *Baeoctenus bicolor* Sæther (Diptera: Chironomidae). J. Fish. Res. Board Can. 34: 2354–2361.

Habrobaenus hudsoni n.gen., n.sp., described from males and a pupa, is related to *Hydrobaenus* Fries sensu Sæther. *Habrobaenus* appears to form the sister group of either *Trissocladius*, or *Trissocladius* and *Zalutschia* combined. The peculiar morphology of the immatures of *Baeoctenus bicolor* Sæther, described here for the first time, probably reflects their parasitic habit on the gills of *Anodonta*.

Key words: *Habrobaenus hudsoni*, *Baeoctenus bicolor*, Diptera, Chironomidae, systematics, larvae, pupae, imagines

SÆTHER, O. A. 1977. *Habrobaenus hudsoni*. n.gen., n.sp. and the immatures of *Baeoctenus bicolor* Sæther (Diptera: Chironomidae). J. Fish. Res. Board Can. 34: 2354–2361.

Habrobaenus hudsoni n.gen., n.sp., décrit à partir de mâles et d'une pupe, est apparenté à *Hydrobaenus* Fries sensu Sæther. *Habrobaenus* semble former le groupe sœur, soit de *Trissocladius*, soit de *Trissocladius* et de *Zalutschia* combinés. La morphologie particulière des immatures de *Baeoctenus bicolor* Sæther, que nous décrivons ici pour la première fois, reflète probablement leurs mœurs parasitaires sur les branchies d'*Anodonta*.

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SÆTHER (1976) revised *Hydrobaenus* Fries and related genera. The genus as well as the immatures of *Baeoctenus* Sæther described below were discovered too late to be included in Sæther (1976), but would otherwise have belonged there.

Methods and Morphology

The mounting procedure used is outlined by Sæther (1969, p. 1). The general terminology follows Sæther (1971a, 1974, 1976, 1977). Measurements and ratios follow Schlee (1966) with additions and modifications given by Sæther (1969, 1976). The holotype of *Habrobaenus hudsoni* n.sp. is deposited in the Canadian National Collection (CNC) in Ottawa.

Habrobaenus n.gen.

Type species: *Habrobaenus hudsoni* n.sp. by original designation.

MALE IMAGO

Diagnosis — Eyes naked. 13 flagellomeres; antennal groove reaching flagellomere 3; flagellomeres 2, 3, and 13 with sensilla chaetica. Temporal setae consisting of outer and inner verticals and postorbitals of about same size. Tentorium parallel-sided posteriorly, with large posterior pit and a few microtrichia. Palp 5-segmented, last segment about 1.3 times as long as third, with 5 apical sensilla chaetica. Antepronotum well developed, median lobes at most in contact at a point anterior of scutal projection. Dorsocentrals normal, acrostichals absent. Scutellars in single transverse row. Wing membrane void of setae, with strong punctation of microtrichia. Anal lobe relatively well developed. Costa not extended; R_{4+5} ends distad to M_{3+4}; An ends distad to FCu; Cu_1 curved; R_{4+5} and R_1 with setae. Squama fully fringed. Sensilla campaniformes about 9 at base of brachiolum, 3 below seta, and about 9 at apex of brachiolum; 3 on subcosta; 1 on FR, and 1 at base of R_1. Pulvilli present and well developed. Comb present. Pseudospurs present on ta_1 and ta_2 of middle and hind legs. Sensilla chaetica apparently absent on all legs. Leg ratios relatively low. Setae of tergites scattered without any obvious pattern. Anal point reduced to a hump with microtrichia and setae. Phallapodeme well developed. Transverse sternapodeme normal. Gonocoxite with small basal lobe. Gonostylus triangular with short, pointed, outer projection and long apical spine.

[1]Present address: Museum of Zoology, University of Bergen, N-5014 Bergen, Norway.

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PUPA

Diagnosis — Frontal seta present, on low tubercles; frontal plate rugulose without "warts." Thoracic horn long and slender, pointed, with weak spines.

Three precorneal setae of about same length. Thorax and wing sheath smooth. Tergite I (TI) with posteriolateral shagreenation; T II–VI strongly and nearly completely shagreenated; T VII–IX with finer, but nearly complete shagreenation. Sternite I (SI) without, S II–III with anteriomedian, S IV–V with anterior and caudolateral shagreenation, S VI–VIII as T VI–VIII. T VII–VIII and S VII–VIII with numerous small posteriomedian spines. T II with numerous caudal hooklets (more than 100). Integument II–IV, IV–V, and V–VI each with numerous spinules in about 10 rows; integument VI–VII with finer spinules in about 8 rows. Pedes spurii B present. Pedes spurii A present on S IV–VI. Segments II–VII with 4 lateral setae; segment VIII with 5 lateral setae; all filamentous on VII and VIII. Genital sac of male very long and slender, extending far past anal lobes. Anal lobe with fringe of long setae, but without any anal macrosetae.

SYSTEMATICS

Sæther (1976: 14–22) calculated the evolution index (Illies 1960) and the adjusted evolution index (Sæther 1970) by assigning the different recognizable anagenetic steps of a number of trends different numbers, starting with one for the most plesiomorphous and proceeding to the highest number for the most apomorphous. The arithmetic mean of the step values of all trends gives the evolution index. The adjusted evolution index is derived by giving all trends and steps equal value regardless of the number of steps, i.e. instead of using the scale 1–5 when there are 5 steps each number is adjusted to a scale of 1–2. If the same trends and steps (Sæther 1976: 16–22) are used for *Habrobaenus hudsoni* n.gen., n.sp. with the addition of one apomorphous trend for the pupa (the lack of anal macrosetae), the evolution indices for the male, the pupa, and the male and pupa combined will be 1.98, 1.67, and 1.88 respectively; the adjusted evolution indices will be 1.63, 1.42, and 1.56. This is very similar to most members of *Zalutschia* Lipina (Sæther 1976, fig. 3).

The kladogenesis, or phylogenetic branching, of the genera studied by Sæther (1976) was illustrated in a scheme of argumentation and by a means of a number of trends (Sæther 1976, fig. 4, p. 23–27). Trends 64–66 in Sæther (1976: 26): absence of acrostichals, distinct curvature of Cu_1, and elongated apical spine of gonostylus, appear to be synapomorphous for *Trissocladius* Kieffer and *Habrobaenus* n.gen., while only trend 58 (the absence of pupal frontal "warts") appears synapomorphous for *Zalutschia* Lip. and *Habrobaenus*. Trends 76 and 77 are synapomorphous for *Trissocladius*, *Zalutschia*, and *Habrobaenus*, but not 75 and 78. Only trend 78, subject to parallelism, may be synapomorphous for *Hydrobaenus*, *Oliveria*, and *Habrobaenus*. The evidence of the female genitalia and of the larva is needed to give any definitive judgment of where to place *Habrobaenus*. However, as trends 64–66 and trends 75–78 are fairly important and nonambiguous, the genus appears to form the sister group either of *Trissocladius* or perhaps of *Trissocladius* and *Zalutschia* combined.

The male imago of *Habrobaenus* will not key out in Sæther (1976: 33) because of the presence of well-developed pulvilli. If this character is neglected, however, the genus will key to couplets 8–9, i.e. to the genera *Trissocladius* Kieff., *Paralimnophyes* Brundin, and *Limnophyes* Eaton. It resembles *Trissocladius* in the hypopygium, but differs in having a well-developed tibial comb, different anal point, and normal palp. *Habrobaenus* has a normally developed antepronotum as in *Paralimnophyes* and less strongly developed than in *Limnophyes*, but has a hypopygium resembling that of *Limnophyes* except for the gonostylus.

The pupa of *Habrobaenus* will not key out in Sæther (1976: 37) because of the absence of anal macrosetae. Aside from this character the genus keys to couplet 11 with *Trissocladius* Kieff. from which it differs by having pedes spurii B and lacking frontal warts, and *Paratrissocladius* Zavřel, from which it differs by having extensive shagreenation on T VII and VIII, and again by lacking frontal warts.

Habrobaenus hudsoni n.sp.

MALE IMAGO (n = 2–3, EXCEPT WHEN OTHERWISE STATED)

Total length 3.15–3.25 mm. Wing length 1.84–1.90 mm. Total length/wing length 1.69–1.71. Wing length/length of profemur 2.68 (1). Thorax with light-brown ground color; vittae, part of anepisternum II and of anepisternum, scutellum, and postnotum black. Legs with forecoxa, trochanters and basal part of femora pale; remaining parts brown. Abdomen dark brown.

Head (Fig. 1A) — Flagellomeres 2–6 wider than long, remaining flagellomeres longer than wide. AR 1.00–1.38. Temporal setae 9–11, including 3–4 postorbitals, 3–4 outer verticals, and 3–4 inner verticals. Clypeus with 5–8 setae. Cibarial pump, tentorium, and stipes as in Fig. 1A. Tentorium 154–176 μm long, 34–37 μm wide, width anterior of posterior tentorial pit 12 μm, distance from apex to posterior tentorial pit 56–60 μm. Stipes 132–148 μm long. Ocelli absent. Palp lengths (micrometres): 32–38, 44–50, 110–130, 100–102, 166–168.

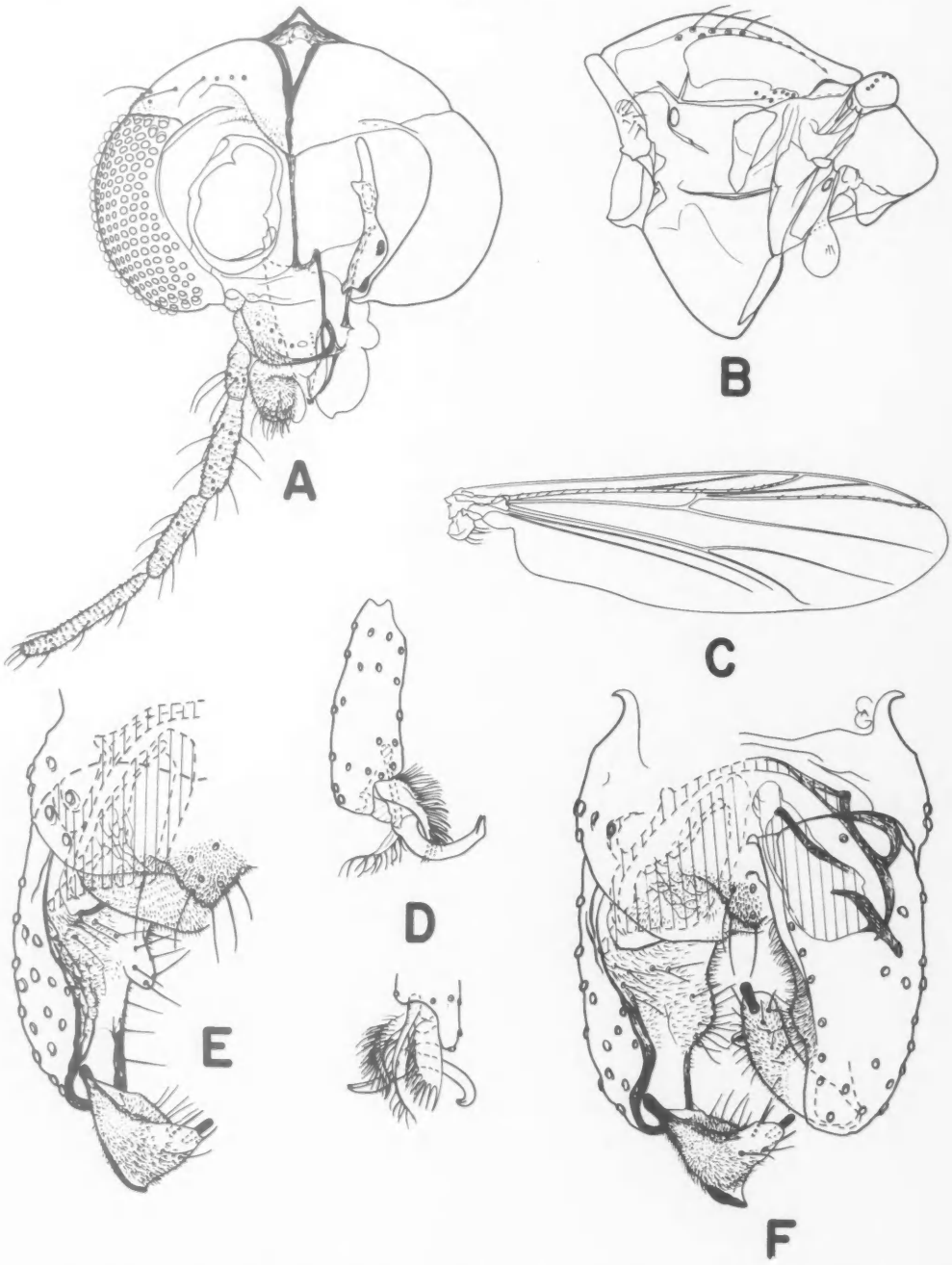

FIG. 1. *Habrobaenus hudsoni* n.gen., n.sp., male imago. A, head; B, thorax; C, wing; D, ta_5, claw, pulvilli, and empodium; E, hypopygium of paratype; F, hypopygium of holotype.

Thorax (Fig. 1B) — Antepronotum with 4–9 setae. Dorsocentrals 10–11, prealars 5–7. Scutellum with 6–10 setae.

Wing (Fig. 1C) — VR 1.14–1.20. Brachiolum with 1, R with 12–15, R_1 with 4–9, R_{4+5} with 2–12 setae. Squama with 7–12 setae.

Legs — Spur of front tibia 58–64 μm long, of middle tibia 38–43 μm and 32–38 μm, of hind tibia 68–76 μm and 34–38 μm. Width at apex of front tibia 42–44 μm, of middle tibia 38–43 μm, of hind tibia 48–58 μm. Tarsal pseudospurs 2 on ta_1 of p_2 and p_3, and ta_2 of p_2; 1 on ta_2 of p_3; 26–36 μm long. Sensilla chaetica apparently absent. Pulvilli as in Fig. 1D. Lengths (micrometres) and proportions of legs:

	fe	ti	ta_1	ta_2	ta_3	ta_4
p_1	771–773	859–938	558–570	343	202–209	129
p_2	711–822	773–846	294–331	165–190	110–123	76–86
p_3	803–883	969–1024	521–534	319	202	98–110

	ta_5	LR	BV	SV	BR
p_1	76–80	0.61–0.66	2.86–2.96	2.75–3.03	2.91 (1)
p_2	63–67	0.38–0.41	4.05–4.42	4.77–5.06	2.53 (1)
p_3	63–76	0.52–0.54	3.31–3.52	3.48–3.57	4.58 (1)

Hypopygium (Fig. 1E, F) — Ninth tergum including anal point with 15–18 setae, laterosternite IX with 5–6 setae. Phallapodeme 84–106 μm long. Transverse sternapodeme 90–117 μm long. Gonocoxite 168–196 μm long, with weak (Fig. 1F) or more pronounced basal lobe (Fig. 1E); gonostylus 84–96 μm long. HR = 2.09, HV = 3.46–3.75.

PUPA (n = 1)

Total length 5.64.

Cephalothorax — Thoracic horn (Fig. 2B) 198 μm long, 24 μm wide, pointed with weak spines. Precorneal setae (Fig. 2B) all about 100 μm long. Frontal seta (Fig. 2A) 150 μm long; on 36 μm high, 22 μm wide tubercle.

Abdomen (Fig. 2C, D) — Shagreenation and chaetotaxy as in generic diagnosis. Tergite II with about 120 caudal hooklets. Longer spinules of pedes spurii A 20 μm long on sternite IV, 12 μm long on V and VI. Anal lobe with 35 filaments in fringe. Genital sac of male (Fig. 2D) overreaching anal lobe by 120 μm.

REMARKS

The smaller holotype has an apparently quite different basal lobe (Fig. 1F) than the largest paratype (Fig. 1E). It also has 12 setae on R_{4+5}, while the largest paratype has only 2. The paratype from Chauga River has a basal lobe about as in the holotype and 6 setae on R_{4+5}. Whether these differences justify a separation into two species can only be evaluated on a greater number of specimens.

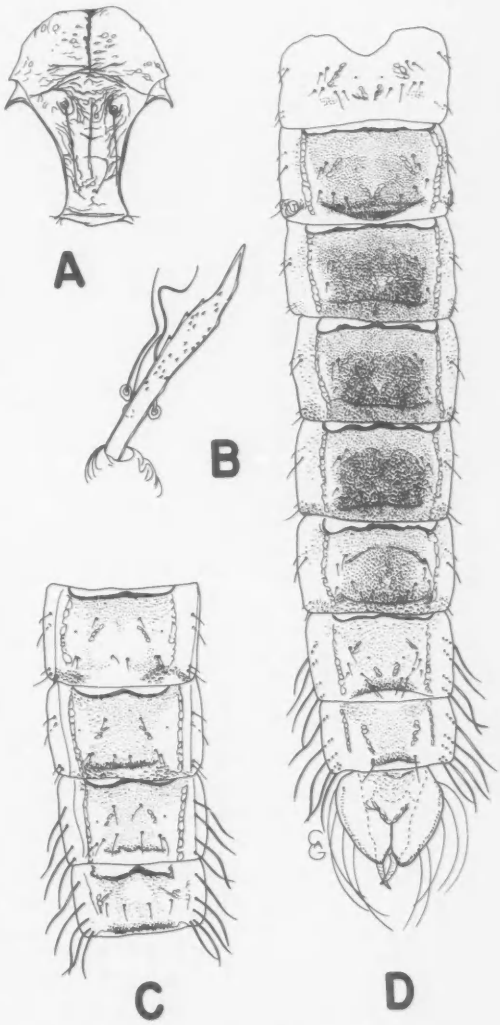

FIG. 2. *Habrobaenus hudsoni* n.gen., n.sp., male pupa. A, frontal plate; B, thoracic horn and precorneal setae; C, sternites V–VIII; D, tergites I–IX.

MATERIAL EXAMINED

Holotype: male with associated pupal exuvium, Chatooga River, Walhalla National Fish Hatchery, Oconee Co., S.C., 15/2/76, P. L. Hudson (CNC No. 15277). Paratypes: male, Wildcat Creek, S.C., 1/5/76, P. L. Hudson; male, Chauga River, Oconee Co., S.C., 23/11/76, P. L. Hudson.

Baeoctenus Sæther 1976

Sæther (1976: 43) described a new genus and species, *Baeoctenus bicolor*, from Lake Winnipeg, Man. Immatures of this genus were never found. Recently Dr C. G. Paterson, Mount Allison University, New Brunswick, sent me some larvae, pupae, and associated imagines of an orthoclad whose larvae were living within the gills of *Anodonta cataracta* (Say) and *Anodonta implicata* (Say). These turned out to be identical with *Baeoctenus bicolor*. Only third and fourth instar larvae were present in the clams from April to mid-June (Gordon et al. 1978). Another very small larva representing an early instar of an orthoclad apparently related to *Phycoidella* Sæth. (Sæther 1971b: 1814) was also frequently found inside *Anodonta cataracata* (Say) (Gordon, et al. 1978). The only species of *Anodonta* Lamarck known to be present in Lake Winnipeg is *Anodonta grandis* Say.

The diagnosis for *Baeoctenus* imagines should be emended as follows: comb reduced to 1 long, heavy, spiniform seta and 0–4 shorter spiniform setae; T IX of female large, triangular to nearly rectangular.

Pupa

Diagnosis — Frontal seta not observed, frontal plate smooth. Thoracic horn long, pointed, densely covered with spinules in apical ¾. Thorax and wing sheath smooth. Tergite I (TI) without, T II with caudomedian, T III–V with median, T VI and VII with anteriomedian to caudomedian, T VIII and IX with anterior shagreenation. Sternites I–VIII with weak anterior to anteriomedian shagreenation. Pedes spurii B barely indicated. Pedes spurii A absent. Segment II apparently with 2 weak lateral setae; III and IV with 3; V–VII with 4; VIII apparently with 2 weak, filamentous lateral setae. Tergite II with numerous, weak, caudal hooklets. Genital sac of male rounded, barely overreaching anal lobe. Anal lobe with 3 heavy, spiniform, straight anal macrosetae; without fringe.

Larva

Diagnosis — Antenna 5-segmented, short and stubby; blade shorter than segments 2–5 combined; ring organ in center of basal segment. S I bifid, with furcation distad of center. S II and S III simple. Pecten epipharyngis consists of 3 simple, sclerotized, pointed, smooth spines. Chaetula basales and laterales all smooth. Premandible with 5 pointed, dark apical teeth and 1 thumb-like, pale, more basal tooth. Mandible with apical tooth longer than combined width of remaining teeth, with seta interna, apparently with very weak seta subdentalis. Maxilla apparently with reduced but broad anterior chaeta, lamelles of galea simple, maxillary palp short. Mentum with 20 teeth, 8 median teeth lighter and at approximately same level, 6 pairs of lateral and often barely distinguishable lateral teeth; ventromental plates elongate, but not very wide. Parapods well developed, but short; a few claws of anterior parapods complex. Procerci low, with about 7 relatively short apical setae, and 2 lateral setae. Supraanal seta about half as long as anal setae. Anal tubules apparently absent.

Systematics

Sæther (1976: 32) regarded *Baeoctenus* as probably closely related to *Hydrobaenus* Fries sensu Sæther, primarily on the evidence of the female genitalia. The imagines of *Baeoctenus* showed the lowest evolution index and adjusted evolution index of any of the genera treated in Sæther (1976, table 1). If another step is added to trends 46, 54–56, and 62 (Sæther 1976: 22), and another trend is added regarding the shape of the anal macrosetae of the pupa, the evolution indices for the pupa and the larva would be 2.20 and 1.44, respectively; the adjusted evolution indices 1.47 and 1.34; the evolution index for all stages combined 1.67; and the combined adjusted evolution index 1.38. The combined indices as well as those for the larva alone are comparable with *Hydrobaenus*, while the indices for the pupa are more comparable with those for *Zalutschia*. *Oliveria* Sæth. is the only other genus treated by Sæther (1976) where the evolutionary level of any immature stage (in both cases the pupa) is higher than that of the imago.

Most of trends 75–83, showing *Trissocladius* plus *Zalutschia* as the probable sister group of *Oliveria* plus *Hydrobaenus* in the scheme of argumentation outlining the kladogenesis in Sæther (1976: 23–27, fig. 4), are found in their plesiomorphous character states in *Baeoctenus*. The exceptions are trends 75, 76, and 82. Of these, trends 75–76 are subject to parallelism and may be ambiguous; trend 82 (reduction of anal lobe fringe) is not directly comparable since this aberrant pupa does not have a fringe at all. In the scheme of argumentation showing the phylogenetic branching of the Orthocladiinae in Sæther (1977: 78–85, fig. 36), trends 3, 4, 39, 40, 47, 48, and 65–74 clearly show that *Baeoctenus* belongs with the genera treated by Sæther (1976). The trends outlining the phylogenetic branching of these genera in Sæther (1977) are trends 41–46 (Sæther 1977: 82). *Baeoctenus* shows the plesiomorphous character states for all of the trends listed under trends 41 including the first two which may possibly belong under trends 43. These trends all are particularly important and show that *Baeoctenus* at least is not most closely related to *Zalutschia* and that it has female genitalia of the *Hydrobaenus* type. However, *Baeoctenus* also shows the plesiomorphous character states for most of the less ambiguous trends 42–44 and 46, while it shows the apo-

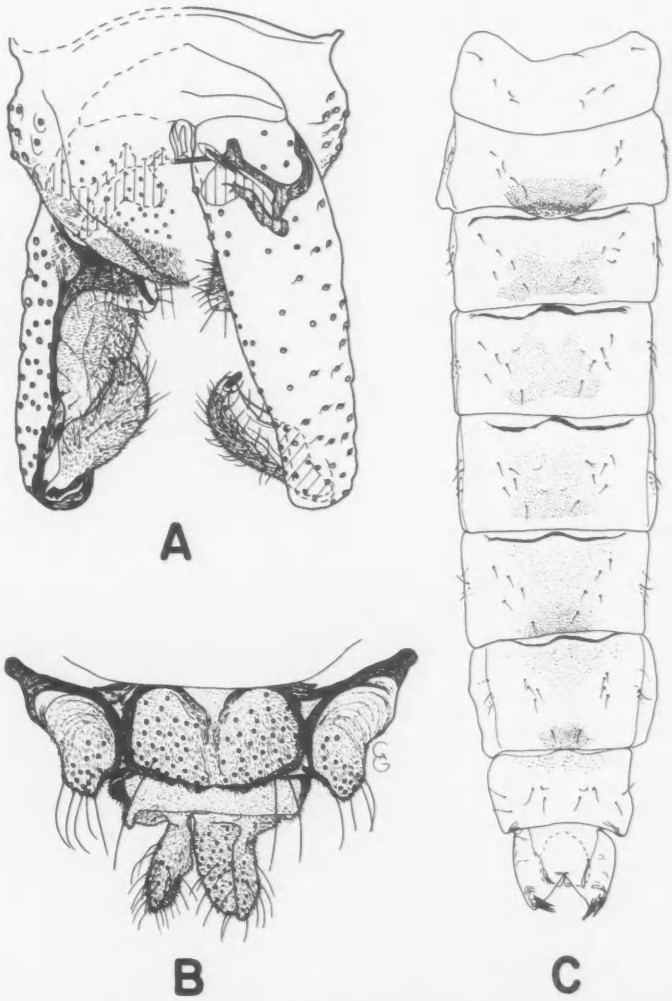

FIG. 3. *Baeoctenus bicolor* Sæth. A, hypopygium of male from New Brunswick; B, genitalia, dorsal view, of female from New Brunswick; C, tergites I–IX of pupa.

morphous states for all trends listed under 45 (i.e. possibly synapomorphy with *Hydrobaenus*). Thus most likely *Baeoctenus* is the sister genus of *Hydrobaenus*, which, however, will mean that of the trends listed under trends 44 only the reduction of the pupal anal lobe fringe may be synapomorphic for *Oliveria*, *Hydrobaenus*, and *Baeoctenus* combined.

The immatures of *Baeoctenus* are rather aberrant as a result of their unusual habitat. The pupa appears to resemble *Chaetocladius* Kieff., but only because of the similar anal macrosetae. The larva has a bifid seta anteriores (S I) different from all the other genera treated in Sæther (1976). However, the furcation takes place in the apical half, not at the base as in other genera with bifid S I, and thus resembles a *Hydrobaenus* larva with the apical branches cut off. The mentum resembles *Epoicocladius* Zavř. more than any other genus, although *Baeoctenus* is not closely related to *Epoicocladius*. *Epoicocladius* is symphoretic on mayflies while *Baeoctenus* lives within the gills of *Anodonta*, and it is tempting to regard the similar menta as a convergence caused by a similar way of living. However, *Baeoctenus* actually eats the gills of *Anodonta* (Gordon et al. 1978), while *Epoicocladius* apparently only combs off algae and detritus on the hairs of Ephemeroptera.

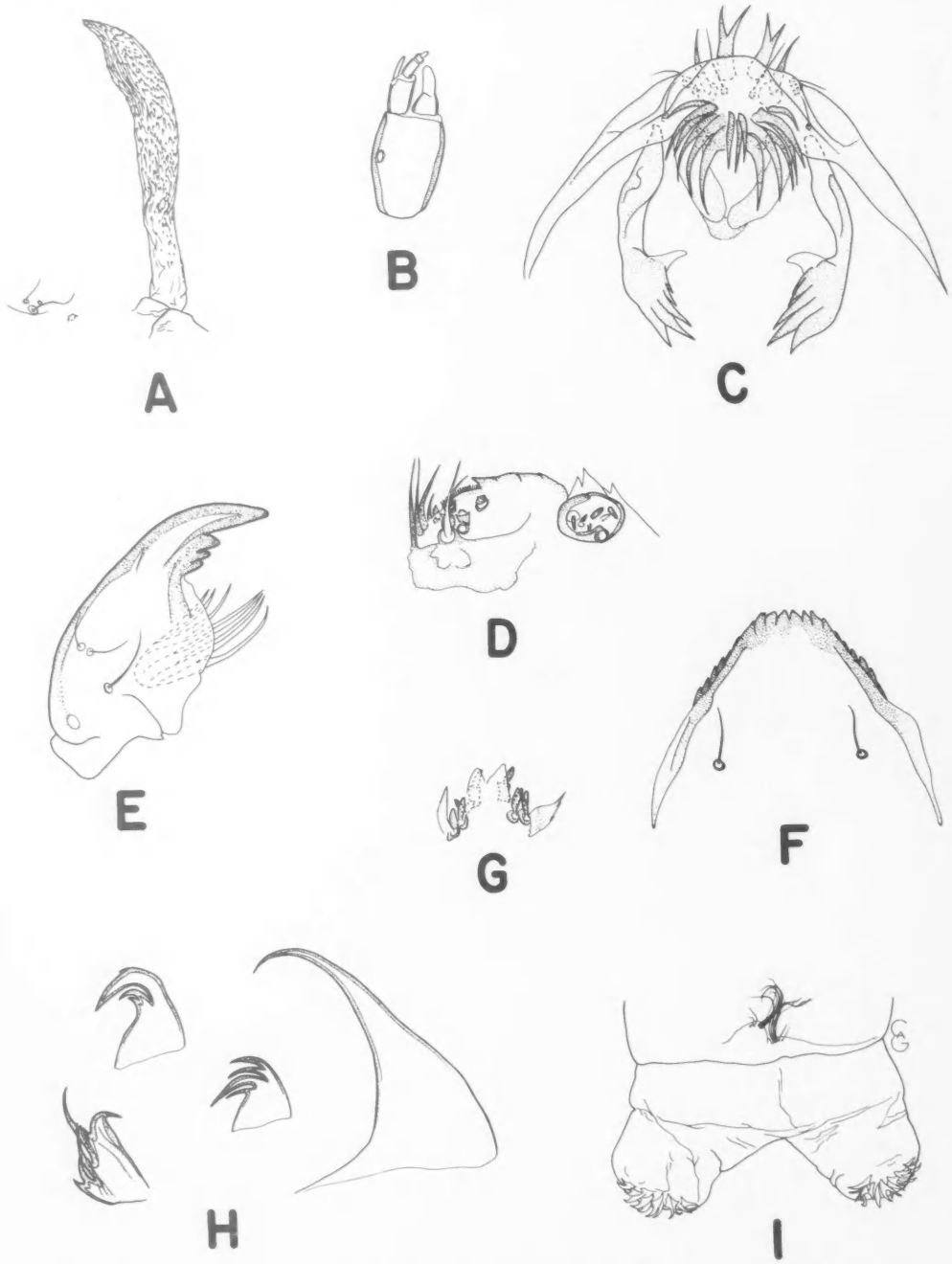

FIG. 4. *Baeoctenus bicolor* Sæth. A, pupa, thoracic horn. B–I, larva: B, antenna; C, labrum including palatum; D, maxilla; E, mandible; F, mentum; G, apex of premento–hypopharyngeal complex; H, claws of anterior parapods; I, apex of abdomen.

Where *Baeoctenus* spends its first two larval instars, however, is unknown.

Baeoctenus bicolor Sæther

Imagines

The adults from New Brunswick conform well to the description by Sæther (1976: 43–46) except for being slightly smaller, the basal lobe of the gonocoxite extending slightly more caudad (Fig. 3A), and tergite IX of the female genitalia being more rectangular than triangular (Fig. 3B). However, one female paratype of *B. bicolor* has a tergite IX intermediate between that illustrated by Sæther (1976), fig. 8H) and that shown in Fig. 3B.

Pupa (n = 2–3)

Total length 8.16–8.44 mm. Length of thoracic horn/length of anal macrosetae 3.51–3.96.

Cephalothorax — Thoracic horn (Fig. 4A) 589–650 μm long, 70–100 μm wide. Precorneal setae (Fig. 4A) weak; anterior one located 18–32 μm from median seta and 26–32 μm from posterior seta; median seta located 16–22 μm from posterior seta; posterior seta located 212–220 μm from thoracic horn. Frontal plate apparently without frontal setae. Dorsocentral setae (dc) 40–58 μm long, anterior dorsocentral seta (dc_1) located 20–46 μm from dc_2, dc_2 located 134–156 μm from dc_3, dc_3 located 20–48 μm from dc_4.

Abdomen (Fig. 3C) — Shagreenation and chaetotaxy as in generic diagnosis. Tergite II with 140–142 caudal hooklets. Longest anal macroseta 164–168 μm long, 18–26 μm wide; other two anal macrosetae 146–158 μm long, 20–22 μm wide. Genital sac overreaching anal lobe by about 15 μm.

Fourth Instar Larva (n = 3)

Total length 6.31–8.97 mm. Head capsule length 0.56–0.59 mm.

Head — Antenna as in Fig. 4B. Lengths of antennal segments (micrometres): 30–34, 10–11, 3, 3, 3–4. AR 1.58–1.61. Basal antennal segment 20–22 μm wide, ring organ in middle. Labrum including palatum as in Fig. 4C. Premandible (Fig. 4C) 62–68 μm long. Mandible (Fig. 4E) 122–136 μm long, with 23–28 μm long apical tooth. Maxilla as in Fig. 4D. Apex of premento–hypopharyngeal complex as in Fig. 4G. Mentum as in Fig. 4F. Postmentum 220–236 μm long.

Abdomen — Anterior parapods (Fig. 4H) mostly with simple claws, but also a few complex. Procercus (Fig. 4I) 40–44 μm high, 32–41 μm wide, with 7 anal setae 240–270 μm long, and 2 lateral setae. Supraanal seta 115–170 μm long, 0.43–0.71 times as long as anal setae. Anal tubules apparently absent. Posterior parapods 260–307 μm long.

Material Examined

Two males, 2 females, 1 mature male pupa, 2 mature female pupae, 3 larvae, Morice Lake, New Brunswick, 2/6/76, C. G. Paterson.

Acknowledgments

I am much indebted to Mr P. L. Hudson, Southeast Reservoir Investigations, Clemson, S.C., for the types of *Habrobaenus hudsoni*; to Dr C. G. Paterson, Mount Allison University, Sackville, N.B., for the material of *Baeoctenus bicolor*; and to Mrs C. A. Galloway for making the drawings.

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Biology of the Morid Fish *Antimora rostrata* in the Western North Atlantic[1,2]

CHARLES A. WENNER AND JOHN A. MUSICK

Virginia Institute of Marine Science, Gloucester Point, Va. 23062, USA

WENNER, C. A., AND J. A. MUSICK. 1977. Biology of the morid fish, *Antimora rostrata*, in the western North Atlantic. J. Fish. Res. Board Can. 34: 2362–2368.

From otter trawl catches in the Middle Atlantic Bight, blue hake, *Antimora rostrata*, were found at depths of 790 to at least 2930 m in the Norfolk Canyon area; maximum abundance was between 1300 and 2500 m. Available data indicate that the blue hake is more abundant in the western than the eastern North Atlantic. Males were smaller in average size than females and a skewed sex–depth relationship was found with a larger percentage of the catch in shallower depths being male. In Canadian Atlantic waters *A. rostrata* live in water at least 500 m shallower. The Middle Atlantic continental slope may serve as a feeding habitat for this species; the reproductive and larval portions of its life history are probably completed in the northern part of its range.

Key words: *Antimora rostrata*, bathymetric distribution, reproduction

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Des traits de chalut effectués dans la gorge du moyen Atlantique ont révélé la présence d'antimores bleus, *Antimora rostrata*, à des profondeurs allant de 790 à au moins 2 930 m dans la région du canyon de Norfolk; l'abondance maximale a été observée entre 1 300 et 2 500 m. Les données disponibles indiquent que l'antimore bleu est plus abondant dans la partie occidentale que dans la partie orientale de l'Atlantique Nord. Les mâles sont en moyenne plus petits que les femelles, et nous avons observée une relation sexe-profondeur biaisée, les mâles formant une proportion plus grande de la prise dans les eaux moins profondes. Dans les eaux canadiennes de l'Atlantique, *A. rostrata* habite des eaux d'au moins 500 m moins profondes. Il est possible que le plateau continental du moyen Atlantique serve d'habitat où cette espèce se nourrit; les phases reproductrice et larvaire de son cycle biologique se passent probablement dans la partie septentrionale de son aire.

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BLUE hake, *Antimora rostrata*, is a common fish of the Middle Atlantic Bight at depths >1000 m (Musick et al. 1975). In his review of the systematic status and nomenclatural problems associated with this morid genus, Iwamoto (1975) stated that for the present it is assumed that only one worldwide species exists, although the taxonomic problems are far from resolved (D. M. Cohen, NMFS Systematics Laboratory, Smithsonian Institution, Washington, D.C. 20560, personal communication).

Although *A. rostrata* is a major constituent of the deep-water fish fauna off the east coast of the United States and its biochemistry is well known (see 1975 Vol. 52B, Comp. Biochem. Physiol.), knowledge of its life history and ecology is almost totally lacking. Most references to this species in the literature are incidental (Haedrich and Horn 1970; Haedrich and Polloni 1974; Markle and Musick 1974; Haedrich et al. 1975; Musick et al. 1975). Cohen (1977) observed and measured swimming speed of this species from the Deep Submersible Research Vehicle *Alvin* at 2400 m in the Middle Atlantic Bight. Iwamoto (1975) described a general biological picture of *A. rostrata* from scanty data and inferences from the biology of certain deep-water macrourids.

The purposes of this report are to describe distributional patterns in detail, to estimate the abundance of the blue hake in the Middle Atlantic Bight, and to compare these estimates with available eastern Atlantic abundance data. Depth distributional changes with latitude and an hypothesis for reproduction in this species are presented.

Materials and Methods

Data from six seasonal cruises from June 1973 to January 1976 in the Middle Atlantic Bight (36°40′ N to 38°40′ N)

[1]Virginia Institute of Marine Science Contribution No. 838.

[2]Adapted from a portion of a dissertation to be submitted to the faculty of the College of William and Mary in partial fulfillment of the requirements for the Ph.D. in Marine Science by the senior author.

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were the basis for our studies. At depths <2000 m, ½-h trawls were made with either a 13.7- or a 9.1-m semiballoon otter trawl, while in greater depths the nets were fished for 1 h (see Musick et al. 1975 for gear dimensions). Mean depth of trawl was calculated from depths obtained every 3 min after the trawl was set (= end of wire pay-out) in 0.5-h trawls and every 6 min in 1-h tows. Unless otherwise stated, depths presented are calculated mean depths. Fishes from successful tows (= net intact and evidence of benthic contact, i.e. the presence of benthic animals, mud, etc.) were measured to the nearest millimetre standard length (SL) at sea except on one cruise where total length (TL) was measured to the nearest millimetre. Total length was converted to SL by the relationship $SL = 0.92(TL) - 0.74$ ($r = 0.99$, $n = 166$). Fresh wet weight was measured to the nearest gram at sea with an Ohaus Dial-O-Gram® scale, which provided a rapid, accurate weight determination even in bad weather. Sex and gonad condition were recorded for all blue hake except those on the June 1973 cruise, and a representative series of gonads was obtained for histological examination and placed in Bouin's or Davidson's fixative (Humason 1972) at sea. On the June 1973 cruise, sex and condition were recorded from a subsample from each tow. In the laboratory gonads were processed by standard histological techniques utilizing Harris hematoxylin–eosin stain. Maximum ova diameters were measured with a calibrated ocular micrometer on either a dissecting or a compound microscope. Analysis of the catch data (expressed as catch per 0.5-h tow) showed the variance to be greater than the mean, so the data were transformed (Elliott 1971). Hydrographic data were collected by CTD or Nansen bottles with reversing thermometers.

Results and Discussion

Distribution and Abundance

Antimora rostrata was captured in every successful trawl from 1190 to 2933 m. A single individual was taken in 792 m of water and represents the only record of this species in our area in depths <1070 m. A trawl at 3080 m, the only one in depths >3000 m, failed to yield any *A. rostrata* among the 82 benthic fishes caught. Depth distribution did not change with season, as has been found for Norfolk Canyon populations of the macrourid *Coryphaenoides rupestris* (Musick unpublished data), nor was there evidence for a relationship between the time of day and the number of blue hake caught. Lack of a relationship may indicate that blue hake do not come off the bottom to forage in midwater like the macrourids *Coryphaenoides rupestris* (Haedrich 1974), *C. pectoralis*, and *C. acrolepis* (Iwamoto and Stein 1974). G. Kreft (Bundesforschungsansalt Surfischerei, Institutfur Seefischerei, Hamburg, Germany, personal communication) has taken a single pelagic specimen (141 mm SL) at 47°45.2′ S, 40°04.5′ W with a 1600 mesh circumference Engel Trawl, which was towed for 0.5-h at a net depth of 2000 m in 5550 m of water.

The area of maximum abundance of *A. rostrata* appears to be between 1300 and 2500 m in Norfolk Canyon with fewer individuals caught outside this range (Fig. 1). Grey (1956) gave a depth range from 402 to 2904 m with the center of maximum abundance around 1800 m. Our results differ in that the blue hake was not found in trawls shallower than 792 m, and the variability in the trawl catches was too great to delineate the actual depth of maximum abundance. The geometric mean (GM), 95% upper (UCL) and lower (LCL) confidence limits and extremes of the number of individuals and their biomass in grams for four depth strata, arbitrarily chosen, are in Table 1.

The blue hake is a dominant member of the benthic fish community from 1300 to 2500 m (Fig. 2), making up 12–95% by numbers and 15–99% by weight of the fishes caught near Norfolk Canyon. In depths <1300 and >2500 m its importance diminishes.

The predictive value of the dominance estimates (Table 1) compares favorably with the few published accounts in the literature. Haedrich and Horn (1970) and Haedrich and Polloni (1974) found *A. rostrata* to make up 27 and 51.5% of the number of fishes caught in trawls made near Hudson Canyon in depths of 1280 m and 1500–1960 m. The 95% confidence limits calculated from Musick et al.'s (1975) data for trawls off the New Jersey coast are

Depth (m)	Numerical (%) $\bar{x}$, LCL, UCL	Biomass (%) $\bar{x}$, LCL, UCL
1143–1353	22.5, 0, 61	32, 0, 68.9
2195–2377	25.4, 0, 53.6	43, 10.9, 75.1

These values fall within the 95% confidence limits of the present study (Table 1).

In 0.5-h bottom trawls by the R. V. *Walther Herwig* for eight stations in West British waters (48°27′ N–61°08′ N) 1–10 specimens were taken in depths from 1200 to 2050 m (GM: 1.8; LCL: 1.1; UCL: 3.1). Catch rates in Icelandic waters (63°13′ N–65°15′ N) with a 42.7 m trawl in depths from 945 to 2026 m ranged from 1 to 18 individuals (GM: 6.4; LCL: 1.6; UCL: 24.5) per 0.5-h tow. The magnitude of the differences in numbers of *Antimora* caught at comparable depths is more striking when the trawls used in the eastern and western North Atlantic are compared. The R.V. *Walther Herwig* fished either a 61- or a 42.7-m bottom trawl, while we used a 13.7-m trawl. Areas sampled by the two German nets are far larger than that of the 13.7-m trawl, yet the 13.7-m trawl consistently caught greater numbers of *A. rostrata*. However, until deep-sea trawls are statistically evaluated, comparisons between different gears should be tentative.

Northern populations of *A. rostrata* along the east coast of North America are found at least 500 m shallower than those off Virginia. Parsons (1976, Fig. 24) reports moderate otter trawl catches from the Nova Scotian slope (44° N) to the slope off Lab-

TABLE 1. Trawl summaries for *Antimora rostrata* from the Norfolk Canyon area. $\bar{x}$ = arithmetic mean; GM = geometric mean; 95% upper and lower confidence limits (CL) follow the means.

	Depth stratum (m)			
	1000–1500	1500–2000	2000–2500	2500–3000
No. of successful tows	10	19	7	7
Temp (°C)	3.9–4.2	3.5–4.0	2.9–3.8	2.3–3.3
Salinity (‰)	35.1–35.2	34.8–35.1	34.9	34.8
GM(CL) no./0.5-h tow	22(10; 51)	24(14; 40)	19(8; 47)	4(2; 8)
Extremes	2–170	3–118	5–57	1–13
GM(CL) biomass (kg)/0.5-h tow	6.5(2.5; 16.7)	11.1(6.4; 33.8)	11.7(4.9; 28.0)	2.6(1.2; 5.8)
Extremes	0.4–62.0	2.4–84.6	3.3–35.5	1.2–9.9
$\bar{x}$(CL) % of catch (numerical)	16.3(4.1; 28.5)	35.7(26.8; 44.6)	67.8(47; 88.6)	25.2(0; 51)
Extremes	1.3–54	11.9–75.7	29.4–95.0	6.3–86.7
$\bar{x}$(CL) % of catch (biomass)	38.4(18.7; 58.1)	54(41.7; 66.3)	82(64; 100)	44.4(13.9; 74.9)
Extremes	1.8–73	15.1–97.3	43.7–99	9.1–93.3
$\bar{x}$(CL) SL(mm) all fish	325(319; 331)	373(368; 378)	398(392; 404)	426(414; 438)
Extremes	175–504	195–545	205–514	245–515
$\bar{x}$(CL) SL(mm) males	316(310; 322)	324(317; 331)	334(318; 350)	321(145; 497)
Extremes	175–557	195–453	243–447	245–386
$\bar{x}$(CL) SL(mm) females	337(325; 349)	386(379; 393)	404(398; 410)	430(420; 440)
Extremes	207–504	223–545	205–517	335–515
$\bar{x}$(CL) % males	59.4(48.9; 69.9)	29.6(17.7; 41.5)	8.6(7.2; 10)	3.7(0; 9.6)
Extremes	37.9–73	7.8–72	6.3–10	0–18

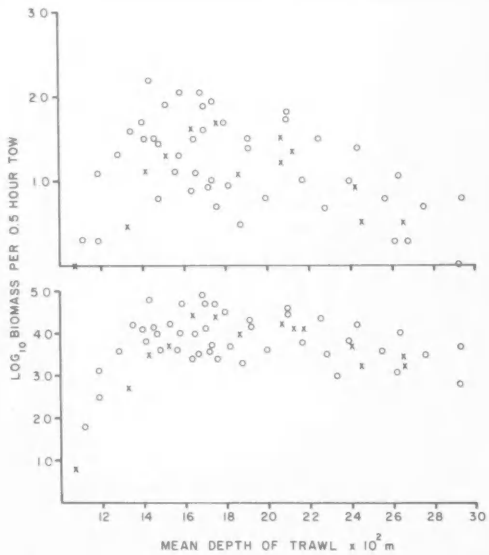

FIG. 1. Depth (m)–$\log_{10}$ catch numbers (*upper*) and biomass (*lower*) of *Antimora rostrata* per 0.5-h tow. Note high variability in catches and area of greatest abundance between 1300 and 2500 m. Open circles, 13.7 m; X's = 9.1-m otter trawls.

rador (60°N) at depths of 457–823 m and the shallowest depth of capture was 229 m on the southwest slope of the Grand Banks. Schroeder (1955) found *A. rostrata* to be more abundant in the northern part of his study area (~43° N) in depths from 659 to 1280 m. Trawls south of this area to the slope off Cape Henry, Virginia (~37° N) resulted in low catches in depths from 730 to 1280 m. Haedrich et al. (1975) present a depth distribution from 900 to 1900 m with a maximum abundance from 1300 to 1600 m on the continental slope off New England (~40° N). Markle and Musick (1974) trawled small numbers of *A. rostrata* from 750 to 1000 m in the northern portion of their study area (38°26′ N–39°50′ N), while none were captured at comparable depths south to 36°24′ N. Musick et al. (1975) found the depth range to be from 1142 to at least 2562 m with a mode of 1661 m off the New Jersey coast. Greater than 99.5% of the 1883 blue hake used in our study from the Norfolk Canyon area are found from 1190 m to at least 2933 m (Fig. 1). Southwest Atlantic populations of *A. rostrata* show a similar trend with shallower captures off south Georgia (54° S) than off Argentina (36° S) (G. Krefft, personal communication).

SIZE–DEPTH RELATIONS

A size–depth relation exists for *A. rostrata* collected near Norfolk Canyon, with smaller individuals found in the shallower end of the bathymetric distribution (Fig. 3). A one-way analysis of variance was performed on the standard lengths pooled into 100-m depth of capture intervals for depths <2500 m and grouped as one treatment >2500 m. This showed a significant difference ($F = 42.95$, df = 13, 1861) at the 99% level. Scheffe's linear contrast to determine significant difference between treatment means (Guenther 1964) showed two general size-

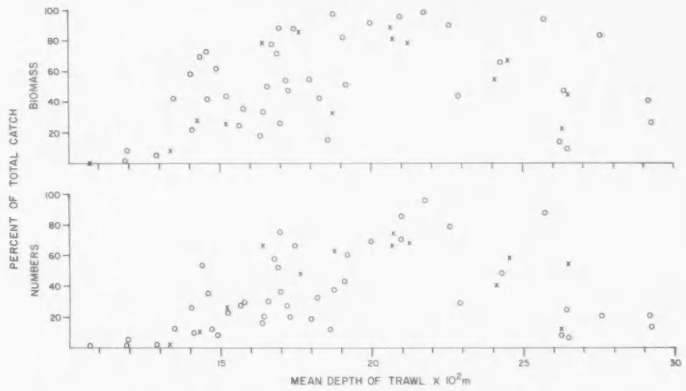

FIG. 2. Plots of numerical dominance and percent of catch by biomass for *A. rostrata* as a function of depth for all cruises. Open circles, 13.7 m; X's = 9.1-m otter trawls.

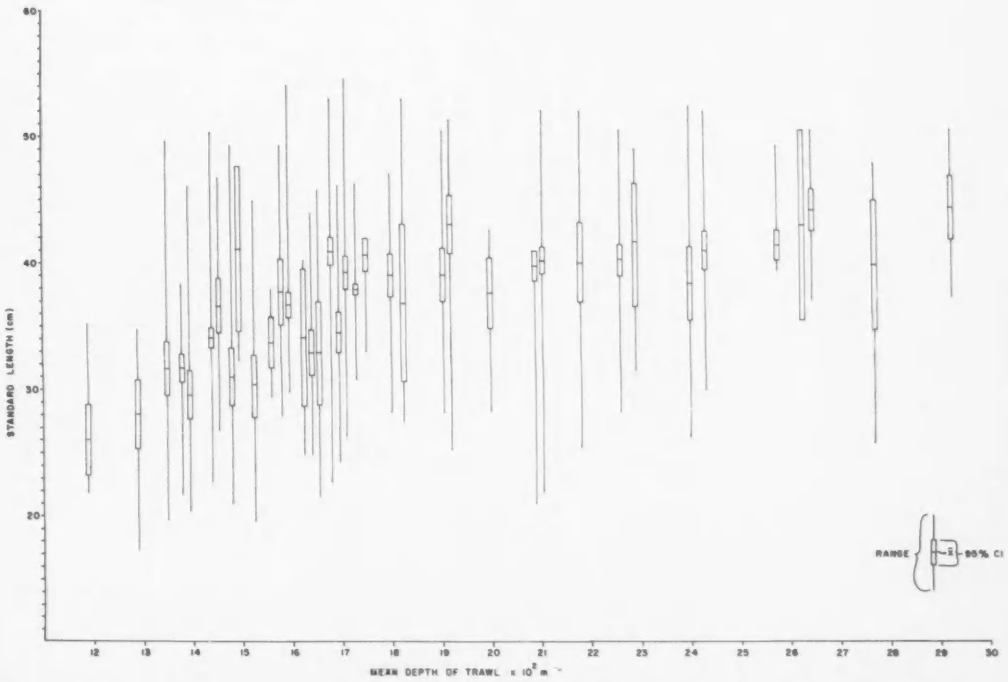

FIG. 3. Size–depth relationship of *A. rostrata* from Norfolk Canyon. Tow times in depths <2000 m = 0.5 h; > 2000 m = 1.0 h. Only 13.7-m trawl values included. The 792-m record and all single and double captures omitted from figure.

groups. *Antimora rostrata* trawled in depths <1600 m were significantly smaller than individuals captured in greater depths. Parsons (1976) found a similar relationship in Canadian Atlantic waters. Fishes trawled at 457–549 m had a mean weight of 140 g, whereas those at 732–832 m averaged 360 g. Longline catches in depths from 1280 to 2377 m gave average values of 600–1600 g. Although the gears are hardly comparable (longlines probably showing bias towards large members of the population), estimated average sizes using the relationship $\log_{10}SL = 1.831 + 0.279\ (\log_{10}W)$ ($r^2 \times 100\% = 96.7$) where SL = standard length in millimetres, W = weight in grams are 457–549 m, 266 mm SL; 732–823 m, 350

mm SL; 1280–2377 m, 404–531 mm SL. Although these data are not statistically comparable to our data they do fit the pattern for Norfolk Canyon (Fig. 3) in that smaller fish are captured shallower than larger fish.

When length frequency distribution of the males is examined (Fig. 4) a partial explanation of the size–depth relationship is seen. Male *Antimora* exceed 50% of the catch in the shallower end of the species' bathymetric distribution, whereas they are almost absent in the deep tows. Since males are smaller than females, this sex segregation helps to explain the size–depth relationship.

Bullis and Struhsaker (1970) found a linear relationship between mean size and depth of capture for several species trawled on the western Caribbean upper slope. Such a relationship could be calculated for the *A. rostrata* data in this paper, but it would mask the actual size variation in a sample (Fig. 3) and fail to show the sex–depth relationship.

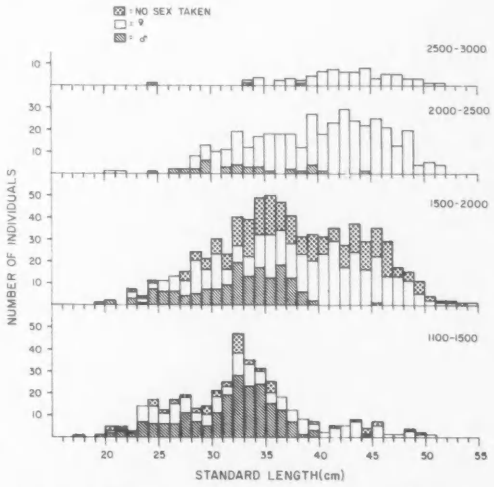

FIG. 4. Length-frequency distribution by sex for *A. rostrata* for four depth strata in the Norfolk Canyon area. Only 13.7-m trawl data included.

REPRODUCTION

Ovaries of *A. rostrata* have a typical gadid type structure (see Vladykov 1972, Fig. 1) appearing as paired fingerlike projections suspended by mesentery from the dorsal peritoneum. The surface of the ovaries is generally darkly pigmented, and in cross section there is an external mesothelial covering, an underlying layer giving rise to the ovigerous lamellae which project into the central lumen. Greater than 90% of the 240 females examined histologically possessed irregularly shaped oocytes ranging from 0.054 to 0.085 ($\bar{x}$ = 0.065) mm in greatest diameter. The nucleus, which is spherically shaped and centrally located, ranges from 0.028 to 0.040 ($\bar{x}$ = 0.03) mm and contains 4–17 small, densely basophilic spherical structures, the protovitellonucleoli of Combs (1969); these are aligned along the interior edge of the nuclear membrane. A few individuals had oocytes of a maximum diameter of 0.12 mm, follicle cells surrounding the vitelline membrane, cytoplasmic vacuoles, and an irregularly shaped nucleus showing the onset of oocyte maturation.

Maturing individuals were rare in our samples with only two females possessing enlarged gonads. One (SL = 512 mm, W = 1325 g) collected in January 1976 had an estimated 1,351,300 eggs ranging from 0.22 to 0.33 ($\bar{x}$ = 0.26) mm in diameter. The ovary made up 2.7% of the weight of the fish. Another, collected in July 1975 (SL = 606 mm, W = 1405 g), had an estimated 760,000 eggs from 0.6 to 0.85 ($\bar{x}$ = 0.68) mm in diameter. The ovary made up 9.3% of the weight of the fish and was noticeably swollen on dissection. Histological sections showed dense eosinophilic yolk granules, well-developed vitelline membranes and follicle cells. Neither atresia nor residual oocytes, which remain in the ovary after spawning, were observed.

In immature specimens, the testes resemble paired, thin, stringshaped structures along the dorsal surface of the peritoneal cavity. They are difficult to distinguish initially but become obvious with close inspection and familiarity. As gonads mature, the testes take on a convoluted gadidlike appearance resembling the testes of the haddock, *Melanogrammus aeglefinis* (see Vladykov 1972, Fig. 6). Only 16 of the 472 male *Antimora* examined showed this testicular development. These developing individuals were collected in all seasons, although the largest number was encountered in September and averaged 352 mm SL (extremes: 233–396 mm).

Histological sections of male *A. rostrata* with convoluted gonads failed to show either the presence of residual spermatozoa in the seminiferous tubules, indicating a recent past spawning, or a large amount of sperm, providing evidence for imminent spawning. All but one specimen with convoluted gonads had primary and secondary spermatogonia.

The absence of smaller fishes and sexually mature adults off the Middle Atlantic States of the U.S. lead us to hypothesize that *A. rostrata* uses the continental slope in this area as a nonreproductive, or somatic, habitat (sensu Markle 1976). Postjuvenile and prespawning adults probably use this geographic area as a feeding ground and later migrate with the onset of sexual maturity. Because the blue hake swims with the same power as the rainbow trout, *Salmo gairdneri*, *A. rostrata* does have the capacity to migrate (Cohen 1977).

There are four possible spawning areas of *A. rostrata*. The Gulf Stream in a region south of Cape Hatteras on the Blake Plateau would provide a

means for egg and larval dispersal and would explain this species' North Atlantic distributional pattern. This idea is improbable, since *Antimora* is rare south of Hatteras and its eggs and larvae have never been taken in the Gulf Stream (D. M. Cohen personal communication). Second, this species may spawn in depths >3000 m. This is essentially untested, as we have made only one trawl at these depths. Third, *Antimora* may rise off the bottom to spawn in midwater. This hypothesis can be discounted for two reasons. If *Antimora* did spawn in midwater, Kreft and his coworkers should have captured many more than one individual during their extensive midwater sampling. Also, maturing gonads would have been observed during our sampling program. Fourth, *A. rostrata* may spawn in the northern part of its western North Atlantic geographical range. Although the eggs and larvae are unknown, the small size of maturing eggs and relatively high reproductive potential suggest that the eggs are pelagic and that the larvae probably spend time in the pelagic realm. An area of relatively high organic productivity is more conducive to larval survival and growth than the relatively sterile areas overlying the deeper regions of the Middle Atlantic slope.

Podrazhanskaya (1971) suggested that another archibenthic fish, *Coryphaenoides rupestris*, undertook northerly spawning migrations from the Canadian slope to waters off Iceland. She pointed out that the predominating currents would passively transport eggs and larvae to the demersal feeding grounds off Newfoundland. An analogous passive transport system has been suggested by Markle (1975) for *Glyptocephalus cynoglossus*, which uses the upper slope in the Middle Atlantic Bight as a nursery area. The situation is different, however, for Middle Atlantic Bight populations of *A. rostrata*, since there are neither small individuals present in trawl collections from this area nor eggs and larvae in plankton collections. If *A. rostrata* spawned in the northern portion of its geographic range, we would expect that smaller individuals would be encountered in more northerly areas. The smaller average size at 457–459 m ($\bar{x}$ SL = 266 mm) calculated from Parsons' (1976) data for Canadian Atlantic waters, when compared with the average size ($\bar{x}$ SL = 325 mm) of the shallowest Norfolk Canyon collections, lends evidence to this hypothesis. In addition, the predominant currents over the continental slope flow south and west from the Grand Banks towards Cape Hatteras (Webster 1969; Worthington 1964; Gatien 1976) and could transport eggs and larvae.

Similarly in trawls off the Oregon coast, *Antimora* larvae or individuals smaller than 132 mm SL have not been taken. Only two females and one male out of 215 specimens trawled have started to mature (W. G. Pearcy, School of Oceanography, Oregon State University, Corvallis, Oreg., personal communication). The material that we have gathered from available sources agrees since trawls have yielded only relatively large individuals, larvae are unknown, and maturing individuals are rare.

The evidence presented for a northerly spawning migration in *A. rostrata* is conjectural, but we present it as an hypothesis to be tested by investigators with the facilities and opportunity to sample the more northerly reaches of the North Atlantic.

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Storage Life of Refrozen Silver Hake (*Merluccius bilinearis*) Processed as Fillets and Minced Flesh from Thawed, Stored, Round-Frozen Fish

DORIS FRASER HILTZ, D. H. NORTH,[1] BARBARA SMITH LALL, AND R. A. KEITH

Department of Fisheries and the Environment, Fisheries and Marine Service, Halifax Laboratory, Halifax, N.S. B3J 2R3

HILTZ, D. F., D. H. NORTH, B. S. LALL, AND R. A. KEITH. 1977. Storage life of refrozen silver hake (*Merluccius bilinearis*) processed as fillets and minced flesh from thawed, stored, round-frozen fish. J. Fish. Res. Board Can. 34: 2369–2373.

Refrozen silver hake (*Merluccius bilinearis*), processed as fillets and minced flesh after thawing of stored round fish that had been frozen within 14 h of capture, underwent rapid deterioration during storage at −18°C compared with once-frozen control materials from the same lot of fish. The estimated maximum storage life of silver hake refrozen as fillets after 3 and 6 mo storage of the round fish at −25°C was reduced to about 4.5 and 1 mo, respectively, from 10 mo for once-frozen control fillets. Quality of the refrozen materials immediately after thawing and refreezing was similar to that of the round-frozen fish, except after 6 mo, where some initial deterioration occurred, particularly in minced flesh. Minced flesh was more unstable in frozen storage than fillets. In all once- and twice-frozen materials, formation of dimethylamine occurred concomitantly with decrease in protein extractability. Round-frozen fish underwent no loss in protein extractability during 6 mo storage at −25°C, but some lipid hydrolysis occurred. These results suggest that the freeze–thaw–refreeze process as applied to silver hake will yield a final product of acceptable quality provided that storage of the round fish does not exceed 3–4 mo and that the refrozen materials are marketed within a month after processing.

Key words: silver hake, *Merluccius bilinearis*, refrozen storage, dimethylamine, minced flesh

HILTZ, D. F., D. H. NORTH, B. S. LALL, AND R. A. KEITH. 1977. Storage life of refrozen silver hake (*Merluccius bilinearis*) processed as fillets and minced flesh from thawed, stored, round-frozen fish. J. Fish. Res. Board Can. 34: 2369–2373.

Des merlus argentés (*Merluccius bilinearis*) recongelés, transformés en filets et en chair hachée après décongélation de poissons entiers entreposés qui avaient été congelés moins de 14 h après capture se détériorent rapidement au cours d'un entreposage à −18°C comparativement à du matériel témoin provenant du même lot de poissons, mais congelés une seule fois. La durée maximale estimée de conservation de merlus argentés recongelés sous forme de filets après 3 et 6 mois d'entreposage du poisson à −25°C diminue à environ 4.5 et 1 mois respectivement comparativement à 10 mois pour les filets témoins congelés une fois. La qualité du matériel recongelé immédiatement après décongélation et recongélation est identique à celle des poissons congelés ronds, sauf après 6 mois, alors qu'il y a début de détérioration, surtout dans la chair hachée. La chair hachée est plus instable dans le matériel d'entreposage congelé que dans les filets. Dans tout le matériel congelé une et deux fois, la formation de diméthylamine est accompagnée d'une diminution d'extractibilité des protéines. Les poissons congelés ronds ne subissent aucune perte d'extractibilité des protéines durant 6 mois d'entreposage à −25°C, mais il se produit une certaine hydrolyse des lipides. Ces résultats donnent à croire que le procédé de congélation–décongélation–recongélation appliqué au merlu argenté donnera un produit final de qualité acceptable, pourvu que l'entreposage des poissons entiers ne dépasse pas 3–4 mois et que le matériel recongelé soit mis sur le marché moins d'un mois après transformation.

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SILVER hake (*Merluccius bilinearis*) of top initial quality can yield primary or secondary fishery products with high consumer acceptability (Peters et al. 1963; Anderson and Mendelsohn 1971; Hiltz et al. 1976). Moreover, this presently underutilized gadoid species has excellent frozen-storage potential, provided the fish are chilled rapidly upon capture, frozen after no more than 2–3 days in chill storage, and maintained at a frozen-storage temper-

[1]Student-assistant, Department of Fisheries, Province of Nova Scotia

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ature of −18°C or below. At higher storage temperatures, or upon temperature fluctuations to levels where enzymatic activity may be stimulated (−10°C or above), the principal deteriorative reaction in silver hake (Hiltz et al. 1976), as in other gadoids (Castell et al. 1971), is the formation of dimethylamine and formaldehyde, with resultant loss of protein extractability leading to textural toughening (Dyer 1973; Castell et al. 1973). Development of rancidity may also occur (Anderson and Mendelsohn 1971). Minced flesh of silver hake, prepared by commercial meat-separators, is more unstable in frozen storage than fillets (Hiltz et al. 1976).

Freezing of round fish at sea (or ashore as soon as possible after capture) for subsequent thawing and processing ensures flexibility in meeting market demands. In addition, this process may be feasible for silver hake because the flesh is susceptible to rapid softening post-mortem and quick processing is needed to maintain high quality. The relatively small size of the fish, average length 30 cm (Jones 1974), makes hand-gutting at sea uneconomic. The fishery has a seasonal nature, with intensive fishing efforts on the Scotian Shelf likely to occur during March–April and July–August (Cadegan and Drebot 1975).

Studies on cod refrozen as fillets have shown that the initial quality of the refrozen product is usually good, being indistinguishable from the once-frozen material (Dyer et al. 1962; Lorentzen 1965; MacCallum et al. 1966; Peters et al. 1968); on subsequent frozen storage, however, deterioration may be rapid compared with once-frozen controls (Dyer et al. 1962).

The present study examines the feasibility of freezing freshly caught silver hake in the round, storing the round fish frozen up to 6 mo, thawing, processing as intact fillets and as minced flesh, refreezing, and storing the refrozen product. Rates of the deteriorative reactions during refrozen storage at −18°C, including dimethylamine (DMA) formation and accompanying changes in protein and lipid constituents, are compared in the twice-frozen flesh with those in once-frozen control samples prepared from the same lot of fish.

Materials and Methods

The silver hake were caught in mid-March 1975, in LaHave Basin by a commercial trawler under charter to the Province of Nova Scotia. The fish ranged from 28 to 60 cm long and were considerably larger than those from 1974 catches used in previous work (23–30 cm) (Hiltz et al. 1976). As the vessel lacked facilities for freezing at sea, several hundred kilograms of round fish were well iced in boxes immediately upon decking and were landed in excellent condition 12 h after capture. Some of the smaller fish were then in rigor.

For preparation of once-frozen control samples, some of the iced round fish were headed, gutted, and washed under commercial conditions within 1 h of landing (13 h since capture); the gut cavities were scrubbed manually to remove the swim bladder, black belly lining, and traces of blood and kidney tissue (Dingle and Hines 1975). The dressed fish were then divided into two lots for preparation of intact fillets and minced flesh, respectively, with representative numbers of large and small fish in each lot. One lot was filleted and skinned; at the same time, the other lot was passed through a Baader meat-separator (Model 695) fitted with a drum having 5-mm holes. The materials were packaged without delay in small polyethylene bags, packed in 0.5-kg wax-coated cardboard cartons, and quick-frozen in a plate freezer at −40°C for 2 h. Cartons were placed in large polyethylene bags for storage in constant-temperature cabinets at −18 ± 0.2°C. This temperature is within the range of those used commercially in distribution channels and is sufficiently high to permit deteriorative changes to occur within a reasonable time.

The remainder of the round fish, then iced in boxes no more than 14 h since capture, were placed in a single layer in aluminum pans and frozen in a commercial blast freezer at −28°C. They were subsequently enclosed in large polyethylene bags, packed in 50-kg wax-coated cardboard cartons, and stored at about −25°C, the usual temperature in a producer's cold storage.

After 1 wk, 3 mo, and 6 mo storage at −25°C, lots of the roundfrozen fish were thawed in recirculating freshwater at 3–5°C; 4–5 h were required to complete the thawing (little or no ice remaining in the flesh). Thawed fish were immediately dressed, processed into fillets and minced flesh, packaged, frozen, and stored in the manner described for preparation of once-frozen controls. These materials are subsequently referred to in the text as "refrozen fillets" and "refrozen minced flesh."

During frozen storage of the once-frozen and refrozen fillets and minced flesh at −18°C, deteriorative changes were followed at weekly intervals by determining rates of accumulation of dimethylamine-nitrogen (DMA-N), of accompanying decrease in extractable protein nitrogen (EPN), and of lipid hydrolysis (increase in free fatty acid (FFA)) and oxidation (malonaldehyde content) by the methods previously applied (Hiltz et al. 1976). Roundfrozen fish stored at −25°C were also examined for changes in these properties at 1 wk, and 3 and 6 mo, using four composite samples of frozen flesh, each from three fish.

Where possible, linear regression lines were fitted to the data, where x = time in weeks and y = concentration of DMA or EPN; 95% confidence intervals of the mean at the midpoint and at $x = 0$ were calculated. Numbers of samples ranged from 8 to 56; all linear relationships were highly significant ($P \leq 0.001$ for 12 out of 14 groups, and 0.01 in 2 groups). Significant differences in rates of formation of DMA or of loss of EPN among groups were tested by a statistical comparison of slopes of the regression lines according to Youden (1951); where differences were demonstrated, they were significant at $P \leq 0.01$.

Results

Deterioration was negligible in round-frozen silver hake during 6 mo storage at −25°C, and was little stimulated by the thawing and refreezing process. In contrast, extensive deterioration occurred in the refrozen materials and in once-frozen control samples during subsequent storage at − 18°C.

Concentrations of DMA (Fig. 1) increased only slightly in the round-frozen fish over 6 mo at −25°C, and there was no loss of protein extractability (Fig. 2). Thawing and refreezing had little or no effect on DMA formation, and protein extractability also remained relatively unchanged, except in minced samples prepared from 6-mo-frozen round fish, where the initial drop in EPN was about 50%. Unaccountably, initial extractability was reduced somewhat in the materials prepared from 0-mo-frozen round fish, perhaps suggesting an anomaly with this lot, although handling, processing, and refreezing techniques were virtually the same as those used at 3 and 6 mo. Further work is required to confirm this finding.

With subsequent storage at −18°C, all materials formed appreciable amounts of DMA (Fig. 1) and concomitantly underwent extensive loss of protein extractability (Fig. 2), thus confirming the relationship between these two reactions in muscle of silver hake (Lall et al. 1975; Hiltz et al. 1976). Refrozen fillets prepared from 6-mo-frozen round fish deteriorated much more rapidly than once-frozen fillets (DMA slopes 0.77 and 0.18, and EPN slopes 0.27 and 0.04 for R6 and control, respectively; both significantly different at $P = 0.005$). Refrozen fillets from 3-mo round fish showed an EPN loss twice as fast as in once-frozen fillets, although DMA formation was similar in both. Refrozen fillets from 0-mo round fish formed DMA twice as fast as once-frozen fillets; rates of EPN loss were similar in both, but the levels were significantly lower in the refrozen material. In all cases, therefore, the quality loss appears greater in the refrozen than in the once-frozen fillets. In refrozen minced flesh, the rates of change in DMA and EPN were generally similar to those in once-frozen minced flesh, although in samples from 6-mo fish, initial EPN values had already dropped to significantly lower levels. In once-frozen minced flesh, the rates of change in DMA and EPN were over twice as fast as in once-frozen fillets, in agreement with previous data (Hiltz et al. 1976). In the refrozen mince (from 3-mo fish), rates were also faster than in corresponding refrozen fillets, but were the same in refrozen fillets and mince from 0-mo fish.

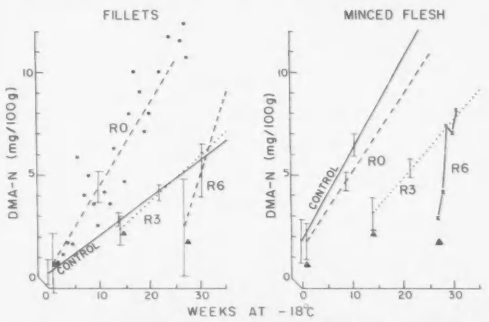

FIG. 1. Dimethylamine formation during storage at −18°C in refrozen silver hake processed as fillets and minced flesh from thawed round-frozen fish stored 0 mo (1 wk) (RO), 3 mo (R3), and 6 mo (R6) at −25°C. Control: once-frozen fillets and minced flesh from the same lot of fish; ▲: round-frozen fish stored at −25°C. Points are plotted for R0 fillets to illustrate degree of scatter.

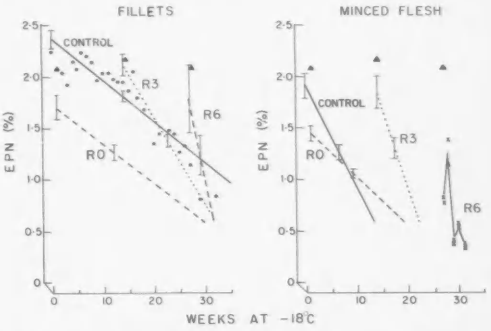

FIG. 2. Loss of extractable protein nitrogen during storage at −18°C in refrozen silver hake materials. Legend as in Fig. 1. Points are plotted for control (once-frozen) fillets to illustrate degree of scatter.

Some lipid hydrolysis occurred in the round-frozen silver hake within the first 3-mo storage at −25°C; at this time, concentrations of FFA were 180 mg/100g, about twice those at 1 wk after freezing (100 mg/100 g). No further change occurred to 6 mo. On frozen storage at −18°C, FFA levels increased steadily, and at rates not significantly different in the once-frozen and 0-mo refrozen materials; moreover, the rates were not significantly different between fillets and minced flesh, as found previously with silver hake stored at −10°C (Hiltz et al. 1976). In the refrozen samples from 3- and 6-mo fish, further accumulation of FFA from the relatively high initial levels immediately after refreezing was slow. Ultimate FFA levels reached, however, were in the same range (250–300 mg/100 g) in all samples, except in minced flesh from 6-mo fish, which formed little FFA on refrozen storage. This may be related to the low initial EPN level in this sample (Castell 1971).

Some evidence of lipid oxidation during refrozen storage was obtained, with malonaldehyde content in a few minced samples rising to 5 μmol/100 g after 1–2 mo. Values in most materials, however, fluctuated widely between 0.2 and 3 μmol/100 g, probably because of a varying proportion of lipid-rich red muscle in the samples analyzed. Slight-to-moderate yellowing of the thawed flesh of the round fish, particularly of the subdermal fatty layer, after 6 mo storage at −25°C was not reflected in increased malonaldehyde content (<1 μmol/100 g).

Total lipid in silver hake fillets average 3.84% (SE ± 0.14 for 77 samples), and was significantly higher

(5% level) than that in minced flesh, 2.72% (SE ± 0.05 for 70 samples), as found previously (Hiltz et al. 1976).

Discussion

Refreezing and mincing of intact flesh (fillets) of silver hake increased the rates of deterioration in frozen storage at −18°C, as measured by changes in the concentrations of DMA and EPN. When the minced flesh was refrozen, however, further changes due to refreezing appeared to be less than those attributable to mincing alone. Reasons for the faster rate of change in twice-frozen compared with once-frozen materials (and in minced flesh compared with fillets) have been discussed by Dyer et al. (1962) as involving the disruptive effect of these processes on cellular structure, with resultant enhanced availability of enzymes to substrates and cofactors. The degradative mechanism producing DMA and its effect on protein stability is also involved. It is interesting that the rate of accumulation of FFA appears to be unaffected by either mincing or refreezing.

Effects of the freeze–thaw–refreeze process on silver hake were similar to those found in other gadoid species, although the data available are limited. Deterioration on refrozen storage at −18°C also developed early and rapidly in trap-cod fillets (Dyer et al. 1962), where extensive quality loss as assessed by taste panel testing occurred within 2 mo of refreezing. Refrozen fillets of trap cod and silver hake deteriorated more rapidly in storage at −18°C than refrozen fillets of trawl-caught cod (Peters et al. 1968); this may be due to proteolytic activity in these "soft-fleshed" species during thawing and refreezing procedures (see Dyer et al. 1962). In the round-frozen state, the gadoid species were stable at low storage temperatures (−23 to −25°C) for up to 6 mo. Immediately after thawing and refreezing, the quality remained unchanged, although on prolonged storage of the round fish (e.g. 6 mo), some initial deterioration occurred in silver hake, as in trap cod (Dyer et al. 1962).

Maximum storage life at −18°C of the once-frozen and refrozen silver hake materials was estimated (Table 1), assuming that the texture would have become unacceptably tough at the EPN value of 0.6 (Dyer 1951). The keeping time for once-frozen fillets (10 mo) compares favorably with a frozen storage life of 12 mo at −18°C reported for top quality dressed whiting by Peters et al. (1968). The table shows clearly that the process of thawing and refreezing appreciably reduces frozen-storage life in fillets and minced flesh of silver hake; the effect is particularly pronounced in materials frozen and stored for 6 mo before processing. (As noted, deterioration rate in once-frozen minced flesh was unaccountably rapid). Results suggest that freezing of silver hake in the round for subsequent thawing and refreezing as fillets or minced blocks may be feasible as a means of preserving surplus catches of this species, provided that storage as round fish does not exceed 3–4 mo to maintain good initial quality after refreezing and that storage of the refrozen materials is minimal (<1 mo at −18°C) to ensure a product of acceptable quality in the marketplace. It must be emphasized that the susceptibility of silver hake to rapid deterioration on chill storage necessitates proper handling of the catch on the vessel or ashore, i.e. rapid chilling, and freezing as soon as possible after capture. The value of such practices in improving acceptability of Cape hake (*Merluccius capensis*) has been demonstrated by Burt et al. (1974).

TABLE 1. Estimated maximum storage life at −18°C of silver hake refrozen as fillets and minced flesh from thawed round-frozen fish stored up to 6 mo at −25°C.

	Storage life (mo)	
	Fillets	Minced flesh
Once-frozen (control)	10	3
Refrozen (at 1 wk)	7	4.5
Refrozen (at 3 mo)	4.5	2
Refrozen (at 6 mo)	1	0.5

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Simulation Concepts for Fishery Systems

LAWRENCE E. GALES, JAMES A. BUSS, AND L. J. BLEDSOE

Center for Quantitative Science in Forestry, Fisheries, and Wildlife, University of Washington, Seattle, Wash. 98195, USA

GALES, L. E., J. A. BUSS, AND L. J. BLEDSOE. 1977. Simulation concepts for fishery systems. J. Fish. Res. Board Can. 34: 2374–2380.

Computer models for analysis of fishery systems may involve complex applications of mathematics and computer science. While the mathematical aspects of these models have been thoroughly studied, less attention has been paid to methodologies for their computer implementation. As a result, some models excessively simplify fishery systems to avoid difficulties in implementation. This study presents an advanced computer technique (linked lists) which permits the inclusion of complex time simulations and data structures in fishery models with little additional effort. Examples of application to complex information arrays and an age-structured population model are included.

Key words: computer, simulation, model, fishery, FORTRAN, ecosystem

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Les modèles sur ordinateur servant à l'analyse de systèmes de pêcheries comportent parfois des applications complexes des mathématiques et de l'ordinatique. Les aspects mathématiques de ces modèles ont été étudiés à fond. Par contre, on a accordé moins d'attention aux méthodes de mise en application sur ordinateur. Comme résultat, certains modèles simplifient à l'extrême les systèmes de pêcheries afin de contourner les difficultés de leur mise en application. Le présent article décrit une technique d'ordinatique avancée (listage enchaîné) permettant d'inclure, avec très peu d'effort supplémentaire, des simulations chronologiques et des structures de données complexes dans les modèles de pêcheries. Les auteurs donnent des exemples d'application de cette technique à des ensembles complexes d'information et à un modèle de population d'âge structuré.

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COMPUTER simulation is increasingly used as a basic tool for the analysis of fishery systems. This technique, however, is often limited by computer languages that are inappropriate for the simulation of real fishery or ecosystem phenomena. Use of such languages sometimes increases the complexity of models to such a degree that important biological mechanisms are slighted. For example, age-structured population models are quite cumbersome (see Lett and Beamish, 1975; Rudd 1975) and some formulations go to great lengths to avoid them (for example Graham 1935; subsequent adaptations such as Schaefer 1957; Pella and Tomlinson 1969). While such simplifications are often justified and highly desirable, they sometimes lead to simulated ecosystem dynamics that reflect the limitations of the model rather than the biological phenomena they are designed to represent.

This is particularly true in large-scale simulations, such as might be required for studies of stream enhancement projects for anadromous species or the interactions of diverse vessel types in a multinational, multispecies, multigear fishery. Here the need is to access large amounts of data, for example, lists of characteristics associated with such categories as vessel types, species fished, locations fished, ports visited, and gear used. The usual way to represent such data is through the array structures of FORTRAN or similar languages (including simulation languages such as GPSS or DYNAMO). However, such structures may be quite wasteful of computer memory and time in this type of application and may impose certain conceptual and programming difficulties that must be compensated for with considerable effort.

This paper describes an alternative method of information organization (called linked lists) for computer simulation of fishery-related systems. We will explain the approach in general and with respect to two examples, a large-scale information and simulation system for northeast Pacific fisheries (NEPAC model) and a food chain for the North Sea (Steele 1974). The rationale for our work lies in past experi-

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ence with simulation of large-scale fishery systems via the GAMES model (Parks 1975; Gales 1972), and in other resource system simulations (Bledsoe and Katz 1976).

If the only objective were the conservation of computer memory, there would be little point to the proposed alternative; however, it has been pointed out that one of the principal values of model building is in terms of organization of ideas (Van Dyne and Abramsky 1975). We feel that a restrictive method of information organization in a model will also restrict ways of thinking about and analyzing a system. If the reader is willing to believe that detailed models are sometimes avoided because of their additional complexity, then we will show that linked lists provide a framework for incorporating important classes of detail, such as stratified variables or discontinuous time, in a simple and straightforward manner. Such models often follow the original assumptions about a system in a more natural way.

Simulation Concepts and Computer Languages

Some people feel that computer languages are much alike and differ mainly in conveniences or "syntactic flavor." While this may be true across a broad spectrum of applications, it is not true in limited areas, where specialized computer languages may strongly affect concept formation (Krasnow and Merikallio 1963). For example, discrete-event simulation languages such as SIMULA 67 (Birtwistle et al. 1973) or SIMSCRIPT II (Kiviat et al. 1968) provide tools for (a) logically separating the actions of individual objects from the interactions in a system as a whole, and (b) modeling objects, such as fleets or fish populations, which vary in size, number, or relationships as a function of time. These vital simulation concepts are best implemented through data structures called linked lists (Weizenbaum 1962; Birtwistle et al. 1973), which offer far more flexibility in modeling than the more familiar subscripted array structures of FORTRAN.

Because SIMSCRIPT and SIMULA are unfamiliar to many fisheries scientists and are often unavailable or poorly supported at a given installation, we developed a linked-list simulation system based on FORTRAN that draws heavily upon the concepts and nomenclature of SIMULA 67, yet offers the many practical advantages of FORTRAN (use of the system is described in Gales and Buss 1975; the system code, which is written in fairly portable FORTRAN for a CDC 6000 series computer, is given with annotation in Buss and Gales 1977). In the following sections we shall outline the linked-list concept and demonstrate its ability to handle difficult fisheries problems, such as age-structured population models or the interactions of discrete and continuous phenomena in a large scale fishery system simulation.

Limitations of Arrays

The usual way to represent stratified variables in FORTRAN models is through arrays. For example, if fishing effort F is to be stratified by vessel type (V), stock (S), fishing area (A), fishing strategy (T), and month (M), then F(6,7,4,2,3) might represent fishing effort for vessel 6, on stock 7, in area 4, using strategy 2, in month 3. However, since very few (sometimes $<1\%$) of the possible V-S-A-T-M combinations exist at any given time, this method wastes an enormous amount of computer memory, since most of the array consists of zeroes.

A more efficient approach is to structure F as a one-dimensional array, F(1), F(2), ..., F(N), whose elements are limited to those subscript combinations that actually exist. The elements of F are accessed through an indexing function treated as a subscript, i.e. if J($\cdots$) is an index function then F(J($\cdots$)) accesses one element of F. For example, suppose that (2,2,4,1,2), (6,7,4,2,3), and (7,2,4,1,1) are the only existing V-S-A-T-M combinations, and function J is constructed such that J(2,2,4,1,2) $\rightarrow$ 1, J(6,7,4,2,3) $\rightarrow$ 2, and J(7,2,4,1,1) $\rightarrow$ 3. Here, $N = 3$ and F(J(6,7,4,2,3)) is actually F(2). Unfortunately, most such indexing functions apply only to a predetermined set of subscript combinations, whereas simulation often requires subscript combinations that change dynamically with simulated time.

A solution to the latter problem is to construct J as a function that maps array subscript combinations to some number between 1 and N. J is called a hash function (Maurer 1975) and locates an element in F by finding its approximate location first, followed by a relatively short serial search to find its exact location. Such functions do permit dynamic subscript combinations, but are fairly time consuming and increase memory requirements because F must be slightly sparse (70–80% full) and J needs an N element array to match F.

However, the most serious objection to the above techniques is that they do not provide a conceptual framework congenial to model design and can actually inhibit a modeler's ability to realistically represent biological and related phenomena.

A better approach is to represent objects in a model as entities that possess attributes (Gordon 1969). By an entity we mean one member of a class of objects, such as a stock or a fleet, and by an attribute we mean a value that helps characterize and distinguish that entity, e.g. the "number of boats" might be an attribute of a "fleet" entity. This concept can be implemented by conventional arrays (Cohen 1974) where each row of an array represents an entity and each column is an attribute so that F(i, j) denotes the jth attribute of entity i in an entity

array F. For example, if V, S, A, T, M, and amount of effort are considered as attributes of the ith unit of fishing effort, which occupy array columns one through six, then the fishing effort for vessel 6, stock 7, area 4, strategy 2, month 3 is denoted by

$F(i,1) = 6$ (vessel type)
$F(i,2) = 7$ (stock)
$F(i,3) = 4$ (area)
$F(i,4) = 2$ (strategy)
$F(i,5) = 3$ (month)
$F(i,6)$ = amount of effort

However, the array implementation of this approach creates other problems. Since attributes are accessed by subscript, the code tends to be messy and unreadable. If entities with different numbers of attributes are stored as rows in the same array, then small entities consist mostly of wasted space. If, instead, each entity type is stored in a separate array, then in a dynamic environment much storage is wasted, since arrays cannot share memory, e.g. entities cannot overflow A into B even if B is nearly empty. In addition, the process of inserting or deleting entities is absurdly expensive, since all entities below the one inserted or deleted must be physically moved.

While such problems can sometimes be solved with complex and ad hoc programming where each data or memory problem arising is treated as a separate case, a better approach is to use data structures specifically designed for a dynamic environment and that offer a relatively simple and unified approach to the problems of data management and the synchronization of events in a detailed model. Such structures are called linked lists.

Linked Lists

A linked list is a set of nodes connected together by pointers. As an analogy, consider a set of knots tied in a string. Each knot represents a node, and a length of string between adjacent knots represents a pointer. Thus, the pointers hold the nodes in the list together much as a string holds the knots together. A node is a data structure that describes an entity, such as a stock or a fleet, in the system to be simulated, and consists of a one-dimensional array of contiguous computer words, each of which is an attribute. Some of the attributes are pointers, i.e. words containing the address of the (logically) next node in sequence. Thus, logically adjacent nodes need not be physically adjacent, but may be scattered all over memory, since the pointers entirely determine the node sequence. The concept is illustrated by the diagram in Fig. 1 and the equivalent computer implementation in Fig. 2.

Linked lists are well suited to dynamic environments. For example, nodes can easily be inserted or deleted in lists by changing a few pointers (Fig. 3) regardless of the size of the list; different data types,

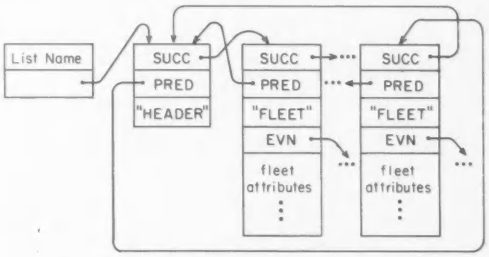

FIG. 1. A linked list containing fleet entity nodes. The first four attributes of each node are system attributes which point to the succeeding node (SUCC), the preceeding node (PRED), identify the type of node (in this case FLEET), and point to a special node (EVN) in the sequencing set (Fig. 4). The remaining attributes are values, such as the number of boats, catchability coefficient, gear type, etc., which characterize a fleet. The first node in the list, after the list name, is called a "header" node and is always present, even when the list is empty.

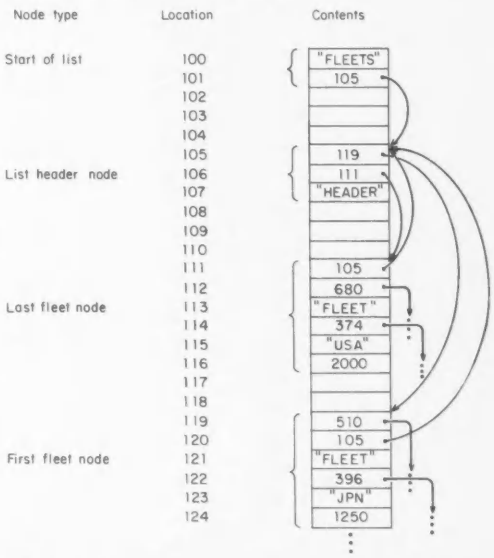

FIG. 2. Section of a computer array used to implement the linked list illustrated in Fig. 1. Each box represents one word in the array. Pointer attributes are indicated by arrows as well as by addresses. Blank words are not part of the list. Note that, in this instance, the fleet that is first in the physical array is last in the list, and conversely, the fleet that is last in the physical array is logically first in the list.

such as real numbers or character strings, can easily be stored in the same node; and different node types, i.e. those representing different types of entities, can be stored in the same list. When an entity is discarded from the model, the space occupied by its node is automatically recycled when the system needs new nodes. Thus, the problem of fixed parti-

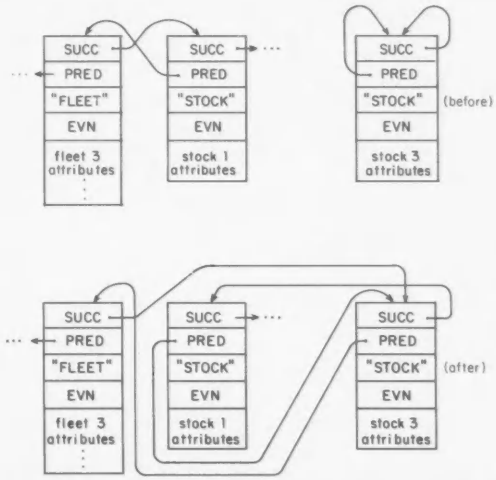

FIG. 3. A fragment of a linked list containing fleet and stock entity nodes (a) before an unattached stock 3 node is inserted; and (b) after stock 3 is inserted in between fleet 3 and stock 1.

tions in storage is eliminated, since one list may overflow into the space discarded by another list.

REPRESENTING TIME WITH LINKED LISTS

Linked lists are also excellent for representing time in a computer simulation. Whereas most early models were highly aggregated and so were able to treat time as a single continuous variable, more detailed models require a more sophisticated representation of time. For example, bioproduction in a particular fishery model might operate as a continuous process, whereas the movements of fleets or the decisions of regulators might take place suddenly and at irregular intervals. Thus, detailed fishery models need a hybrid timing system that combines and interleaves continuous and discrete processes. The discrete-event scheduler is best implemented by a linked list called the sequencing set (SQS) as shown in Fig. 4.

The discrete-event scheduler operates by moving sequentially from one node in the SQS to the next. When it reaches a given SQS node, the simulation time is set to the event time stored in an attribute of the SQS node named EVTIME. Then the system transfers control to a subroutine associated with the type of entity (e.g. FLEET or STOCK) pointed to by another attribute named OBJ. The subroutine itself operates in zero simulated time. In addition, it may cancel or reschedule its own or other event notices by use of special commands (e.g. CALL ACTVATE, CALL CANCEL, etc.) which insert or delete nodes in the SQS.

Continuous processes operate in small time steps,

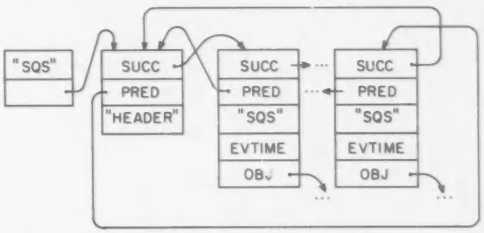

FIG. 4. The sequencing set (SQS). Each node is an "event notice" which specifies the time (EVTIME) when the entity pointed to by OBJ will become active. The EVN attributes shown in Fig. 1 and 2 point back to the event notice whose OBJ attribute points to them.

Δt, between discrete events, but may also post event notices in the SQS for immedaite activation, if need be.

SYSTEM ROUTINES

The list-processing and event-scheduling features discussed above are implemented by fixed prewritten subroutines stored on a library ready for use. A representative subset of these routines is described below:

GETATTR(P): This routine retrieves all user-defined attributes from an entity node pointed to by P and stores them in a FORTRAN-labeled common block where they may be manipulated like any other variables. GETATTR provides a useful subscript free notation, which considerably simplifies code.

PUTATTR(P): This routine is the inverse of GETATTR in that it returns the (possibly modified) variables retrieved by GETATTR back into node P.

HEADER(P): This is a logical function which returns the value "true" if, and only if, P points to a header node.

FIRST("name"): This function returns a pointer to the first actual node (not the header node) in the list "name"; i.e. P = FIRST ("name") points to the first node in the list "name."

SUCCF(P): This function points to the node logically following P in a list.

PREDF(P): This function points to the node logically preceeding P in a list.

GNEW("name"): This function creates a new node of the size needed for en-

tity type "name", and returns a pointer to the new node; i.e. P = GNEW("name") creates a node pointed to by P.

DISCARD(P): This routine delinks node P from its current list (if any) and saves it for recycling. At a later time, this storage space may be used to fabricate new nodes.

ACTVATE(P,T): This routine posts an event notice in the SQS for node P at time T. As a result, the subroutine associated with node P is executed when the system time advances to time T.

Examples

Example from the NEPAC Simulator

The NEPAC simulator (Gales and Buss 1975; Bledsoe et al. 1974; Buss et al. 1977) is a large multispecies model being used to explore various fishing and regulatory strategies for fisheries in the northeast Pacific. We present here a small submodel abstracted from NEPAC that illustrates the use of linked lists and the simulated interaction of discrete and continuous phenomena. The continuous process modeled is that of fishing, which operates in small constant Δt time steps (of perhaps one simulated day) in between discrete events. The discrete events include the attainment of critical values, such as the capacity of a fleet being reached, which require attention by the scheduler. Discrete events occur at irregular multiples of Δt and might be spaced (simulated) months apart.

This example makes use of two linked lists to represent fleets and stocks, which are illustrated in Fig. 5. The fishing process is illustrated in the flow chart and equivalent FORTRAN code in Fig. 6 and Table 1.

List Processing Applied to Steele's Model

Steele (1974) presents a simple model for the population dynamics of copepods, which takes into account the vertical mixing of water, the nutrient cycle, grazing by copepods, growth rates, and predation by herbivorous copepods. It avoids the complexities of most age-structured computer models by restricting the population to a single cohort and is largely defined by four differential equations.

We extended Steele's model by incorporating an age structure into the copepod population. The age structure is introduced via linked lists, where list nodes correspond to age cohorts and attributes are the characteristics of each cohort — age, average weight (W), and population density (Z). New and old cohorts enter and leave the model more or less continuously. The linked-list structure is shown in Fig. 7.

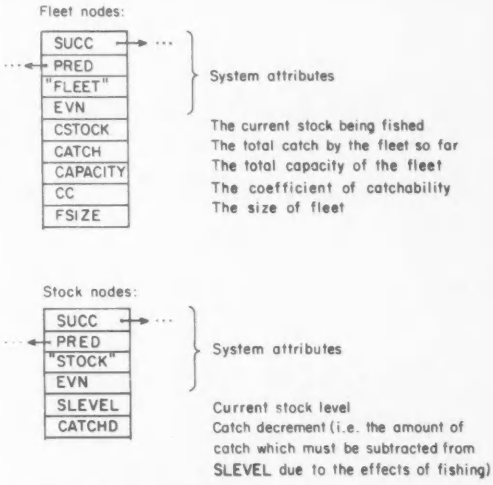

FIG. 5. The fleet and stock nodes used in the NEPAC model.

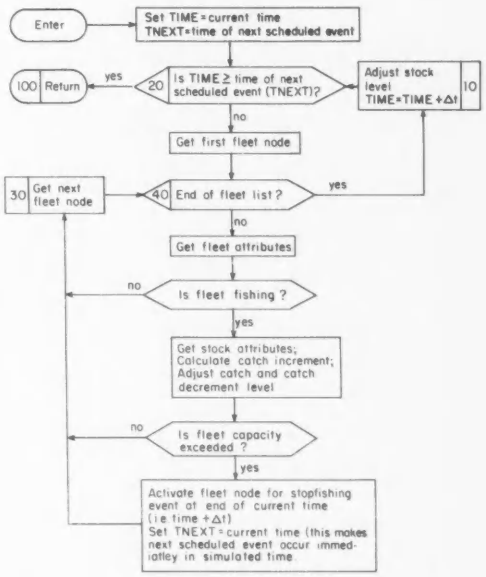

FIG. 6. Example of a continuous model that simulates the process of fishing.

The linked-list technique allowed us to extend the model without violating Steele's goal of a model which contains only the bare essentials for a dynamic and functional description of the North Sea food web. The extended model reproduced the population dynamics much more realistically, yet required only two additional input parameters. The

TABLE 1. A complete subroutine, except for data declarations, which simulates the continuous process of fishing.

Code	Comments
SUBROUTINE CNTNOUS(DT)	DT is the time increment Δt for the continuous event
...	
TIME = CURRTM	Time of current discrete event
TNEXT = NEXTTM	Time of next scheduled event
20 IF(TIME.GE.TNEXT)GOTO 100	Leave timing loop
Q = FIRST(5HFLEET)	Get the first fleet node
40 IF(HEADER(Q))GOTO 10	Check for end of fleet list
CALL GETATTR(Q)	Retrieve all attributes for this fleet
IF(CSTOCK.LE.0)GOTO 30	Skip if fleet not fishing this stock
CALL GETATTR(CSTOCK)	Retrieve the attributes of the stock being fished by this fleet
CATCHI = DT*SLEVEL*CC*FSIZE	Compute catch increment
CATCH = CATCH + CATCHI	Increment catch
CATCHD = CATCHD + CATCHI	Update catch decrement
CALL PUTATTR(Q)	Put updated fleet attributes back in fleet node Q
CALL PUTATTR(CSTOCK)	Put updated catch decrement back in stock node CSTOCK
IF(CATCH.LT.CAPCTY)GOTO 30	Check for capacity exceeded
TNEXT = TIME	Set exit time to abort this routine and schedule fleet Q for stop-fishing action
CALL ACTVATE(Q, TIME)	
30 Q = SUCCF(Q)	Get next fleet node
GOTO 40	
10 CALL REDUCE	Call a subroutine that cycles through the stock list and sets SLEVEL = SLEVEL − CATCHD; CATCHD = 0; thereby reducing the stock level by the amount of fish caught
TIME = TIME + DT	Increment time by DT
GOTO 20	
100 RETURN	
END	

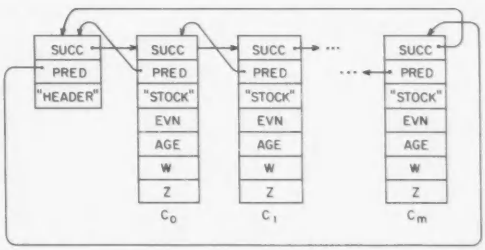

FIG. 7. Cohorts as nodes in a linked list. The first actual list node after the header node, C_0, is not used as a cohort but serves to initialize the values for all new cohorts. The attributes W and Z are the average weight and population density of cohorts, respectively.

entire model consists of five small subroutines, of which Table 2 is a typical example.

Discussion

Information structures, such as languages, notations, or coordinate systems, are not merely passive carriers of information, but are active agents which strongly influence the thoughts of a user, so as to render certain courses of action easy and natural and others difficult and awkward. For example, some problems in physics or mathematics are much more readily handled in polar or cylindrical coordinates than in the more familiar rectangular coordinates. It is perhaps more difficult to perceive when a gradual but progressive quantitative increase in the complexity of a problem brings with it major qualitative changes as well, so that structures that are quite useful in small problems cease to be effective when the same type of problem is extended.

Many early fishery and ecosystem computer models were simple continuous-event simulations which involved only a few highly aggregated parameters. As such, they fit easily into the conceptual frameworks provided by simple simulation languages such as DYNAMO or MIMIC, or algebraic languages such as FORTRAN or ALGOL. However, attempts to extend these models, for example by incorporating more realistic timing mechanisms or more parameters, often led to such complex and inefficient programs that some formulations were forced to abandon important aspects of reality to reduce the complexity of programs to a manageable level.

The linked-list concept presented in this paper, and available in modern simulation languages, readily permits the extension of simple models to more realistic forms, particularly along the lines of discrete–continuous event timing systems, time lags, and large sparse and/or dynamic data structures of the type often required in fishery models.

Now that the linked-list techniques have been

TABLE 2. A sample subroutine from the extended version of Steele's model which implements age structure via linked lists.

Code	Comments
SUBROUTINE GROW(DT)	
. . .	
S = SUCCF(FIRST(5HSTOCK))	Get the first active cohort, C_1, in the list for stocks
10 IF(HEADER(S))GOTO 100	Leave the loop if we are at the end of the stock list
CALL GETATTR(S)	Get attributes for cohort S
CALL DER	
W = W + DWDT*DT	Solve diff. eqn. for W
Z = Z + DZDT*DT	Solve diff. eqn. for Z
M = M + W2*Fl(W, WMIN)*DT*Z*W**0.7	Increment egg production by the number of eggs produced by this cohort
CALL PUTATTR(S)	Save the updated values for W and Z in list node S
S = SUCCF(S)	Get next cohort node in list
GOTO 10	
100 RETURN	

presented in a more familiar and widely available computer language, we hope that more scientists will avail themselves of these powerful simulation concepts.

Acknowledgments

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Grazing of Marine Copepod Developmental Stages on Naturally Occurring Particles

S. A. POULET

Institut national de la recherche scientifique, INRS — Océanologie, Université du Québec, Rimouski, Qué. G5L 3A1

POULET, S. A. 1977. Grazing of marine copepod developmental stages on naturally occurring particles. J. Fish. Res. Board Can. 34: 2381–2387.

Grazing experiments were performed with copepodids (stages CI–IV) of *Pseudocalanus minutus* feeding on naturally occurring particulate matter. Variations in the feeding rate of copepodids were associated with seasonal changes in the standing stock of particulate matter. Copepodids adapted to seasonal variations within the particle spectrum. Particle sizes <22 μm contributed most of the standing stock of particles during the period studied. Maximum consumption was recorded when copepodids fed on small-size particles. The importance of fine particles is illustrated in comparative feeding experiments performed with adults and copepodids fed simultaneously on the same particles. The differences between the mean consumption of copepodids and adults are highly significant in the particle size ranges below 22 μm. The fact that copepodids obtain more food than adults on particles <10 μm is probably related to the smaller mesh size and to the higher frequency of vibration of their mouth appendages. Although all copepod stages are opportunistic feeders, such a mechanism allows copepodids to reduce feeding competition with adults and allows them to fulfil their higher requirements for energy from food particles that have a high productive potential and a high nutritive value. This provides the evidence that feeding niches are partially separated between young and adult copepods.

Key words: calanoid copepods, copepodids, *Pseudocalanus minutus*, grazing, competition, naturally occurring particles

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Des expériences ont été effectuées sur des copépodites (stade CI–CIV) de *Pseudocalanus minutus* nourris de particules naturelles en suspension. Les variations du taux d'ingestion des copépodites sont associées aux changements observés dans le standing stock de la matière particulaire. Les copépodites s'adaptent aux fluctuations saisonnières du spectre particulaire. Au cours de la période considérée, les particules < 22 μm constituaient la majeure partie du stock des particules. L'ingestion maximale des copépodites est enregistrée quand ceux-ci consomment des particules de petite taille. L'importance des petites particules est illustrée par les expériences comparatives effectuées simultanément avec des adultes et des copépodites. Les différences entre l'ingestion moyenne des copépodites et des adultes sont hautement significatives pour toutes les particules < 22 μm. On doit probablement relier ces différences au fait que les copépodites, à l'inverse des adultes, ont des pièces buccales capables de vibrer à de plus hautes fréquences et possédant des mailles plus fines. Bien que les divers stades de copépodes soient tous des opportunistes, un tel mécanisme aboutit à limiter la compétition avec les adultes; tout en leur permettant de satisfaire leurs très grands besoins énergétiques, en ingérant des particules au potentiel productif et de valeur nutritive très élevés. Ces résultats tendent à indiquer qu'une séparation partielle existe entre les niches trophiques des jeunes copépodes et des adultes.

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THE structure of the marine food chain and the morphological limitations dictated by the environment are such that, in general, large particles have to consume smaller ones (Sheldon et al. 1973). In seawater several mechanisms contribute to the formation of small particles in the 1–10 μm range (Sheldon et al. 1967). According to Parsons and Seki (1970), increases in small-particle concentration result from bacterial growth and clumping, aging of phytoplankton blooms, growth of heterotrophic organisms, and grazing. All these processes operate simultaneously under natural conditions. Small particles are numerically abundant, but their concentration is generally low, despite their high production potential, probably because production and consumption are in balance (Sheldon et al. 1973).

Grazing experiments have been performed on

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immature copepods fed on phytoplankton cultures (Gauld 1951; Marshall and Orr 1956; Mullin and Brooks 1967; Paffenhöfer 1971). No work has yet been done on the feeding of immature stages on naturally occurring particulate matter, except very recently by Allan et al. (1977). Experiments are presented here to illustrate the grazing of young copepod stages on the natural-particle spectrum. The production and the nutritive value of small particles are discussed with reference to their utilization by copepodids in competition with adult copepods.

Materials and Methods

The grazing experiments were performed with water samples collected at 5 m depth in a small basin (Bedford Basin, N.S.). Zooplankton was obtained by oblique tows with No. 6 and 20 plankton nets (239 and 76 μm mesh, respectively) towed from 20 m to surface. A mixture of copepodid stages CI–IV, and adult females of *Pseudocalanus minutus* were picked out. Individuals (100 in 1971; 50 in 1972–73) of each category were placed in separate beakers filled with 1 ℓ of seawater previously screened through a 160-μm mesh. On the average, 50–70% of the copepodids used in the experiments belonged to stage CIII. Experiments with copepodids and adults were performed simultaneously, at weekly intervals, to study the feeding in relation to changes in particle spectra. Experiments were done in duplicate in 1972–73. Details of the experimental procedures to determine grazing rates have been described earlier (Poulet 1973, 1974). Particle counts were made with model B and model T Coulter counters (Sheldon and Parsons 1967).

Copepodid stages (CI–III) and adult females were held in cooled petri dishes in a dark room while microscopic observations were made of the mouthparts with a strobe light. When the mouth appendages were in phase with strobe revolutions they seemed to be motionless. The frequency of movements was recorded 3 times for each copepod for successive groups of three to five individuals. Microscopic observations were also conducted to compare the number of setae and the size of each segment of the mouth appendages of adult females and copepodid stage CIII of *P. minutus*.

Results

Figure 1 illustrates the monthly variation in mean concentration of particles in different size-groups. As previously shown (Poulet 1974) the total particle concentration (group 0) changed from one season to another. Except in spring and fall when concentrations of large-sized particles (groups 4–5) were temporarily high, most of the changes in total particle concentrations at other times occurred in small-size categories (groups 1, 2, and 3).

The total consumption by copepodids of particles varied seasonally (Fig. 2, group 0) in roughly parallel fashion to changes occurring in total particulate matter (Fig. 1, group 0). Highest consumption occurred during the spring and summer, and food uptake decreased sharply in early winter.

In size-groups 1–5, particle consumption also varied with concentration (Fig. 1, 2). On average, copepodids obtained relatively little food from large particles (groups 4 and 5) even during spring when particle concentration in these two groups was high relative to the others (Fig. 1). Particles in groups 1 and 2 combined provided 2–6 times as much food as group 3, and much more material than groups 4 and 5 combined, except in early spring of both years.

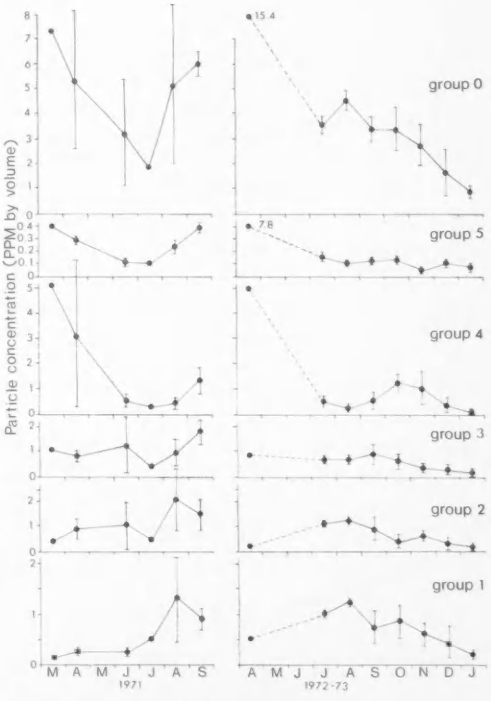

FIG. 1. Monthly variations of the mean particle concentration in water collected from Bedford Basin, N.S., at 5 m depth. Mean and SD's. Size range — group 0: total concentration in the 1.58–144 μm range; group 1: 1.58–3.57 μm; group 2: 4.0–8.97 μm; group 3: 10.1–22.6 μm; group 4: 25.4–57.0 μm; group 5: 64.0–144 μm.

Whatever the particle size-group was, neither monthly mean particle concentration nor monthly mean food consumption by copepodids was significantly different (t-test, $P = 0.05\%$) from one month to another during the summer and part of the fall. In Bedford Basin, the highest concentration of adult copepods and copepodids occurs during the periods of high concentration of small particles (<22 μm) (Fig. 1) despite an intense grazing pressure from copepods (Fig. 2 and Poulet 1974) on those particles; larger particles seem to be preferentially eaten by adults, but small ones grow faster.

The monthly mean food uptake was computed in terms of organic carbon (Table 1). For particulate

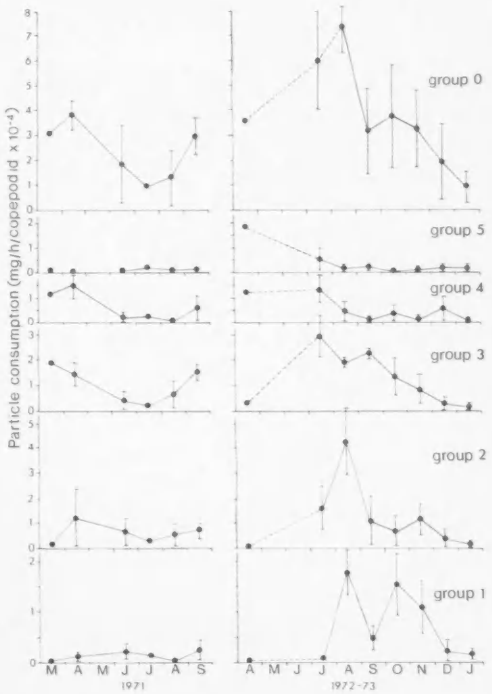

FIG. 2. Monthly variations of the mean particle consumption by copepodids stage CI–IV of *Pseudocalanus minutus*. Mean and SD's. Group 0–5 as in Fig. 1.

Table 1. Summary of grazing experiments with copepodids of *Pseudocalanus minutus* (stage CI–IV). Mean values ± SD's.

Mo.	No. of exp.	Mean food concn. (ppm by vol)	Mean rations (mg C × 10^{-3}· copepodid^{-1}·day^{-1})
Ma.	1	7.37	0.17
Apr.	4	7.83±5.58	0.21±0.03
June	3	3.21±2.20	0.11±0.09
July	5	2.98±1.01	0.20±0.18
Aug.	9	4.80±2.33	0.25±0.07
Sept.	9	4.72±1.49	0.18±0.07
Oct.	7	3.40±0.76	0.21±0.13
Nov.	8	2.75±0.82	0.19±0.08
Dec.	4	1.67±0.88	0.11±0.08
Jan.	4	0.89±0.10	0.05±0.03

material, a mean annual carbon to volume ratio of 0.024 ± 0.014 was computed from Poulet's (1976) data. The mean varied seasonally from 0.05 to 0.25 mg C × 10^{-3}·copepodid^{-1}·day^{-1} (Table 1). However, it was rather uniform during the summer and fall.

The feeding of copepodids was studied in relation to the spectra of particulate matter and compared with the grazing of adult copepods (Fig. 3). Poulet 1974 showed that particle size spectra changed seasonally in terms of number, amplitude, and size range of the peaks (Fig. 3). Copepodids of *P. minutus* took particles of all sizes below 150 μm. Grazing was focused in the same size ranges as the particles causing the peaks. Feeding patterns of copepodids were very similar to the feeding of adult copepods. However, when peaks of large-size particles (~50 μm) occurred, then the uptake by copepodids was negligible compared with adults. On the other hand, the grazing of copepodids on small-size particles within 1.58–20 μm was generally higher than in adults (Fig. 3).

Consumption by adult females and copepodids fed on the same particulate matter is compared in Fig. 4. Consumption was computed on the basis of dry body weights of 9.79 μg·adult^{-1} and 3.26 μg·copepodid^{-1} of a single group of *Pseudocalanus* adult females and a single group of copepodids stage CIII. Even though there were probably seasonal variations in the body dry weight of each developmental stage, the consumption by copepodids of particles in most groups was higher and significantly different from that of the adults, except in groups 4 and 5 (Fig. 4).

Microscopic observations of the mouth appendages showed that the length of the appendages and the number of setae on the appendages are less in copepodids than in adults (Table 2). The volume swept by each appendage was assumed to correspond to a hemisphere the diameter of which equals the total length of the appendage. The ratios N/L and N/V (corresponding to a mesh size per length and volume unit) were computed for both developmental stages (Table 2). Although the hypothetical volume of each appendage is less in copepodids than in adults, the reverse pertains for N/L and N/V (Table 2).

Strobe observations demonstrated that vibrations of the feeding appendages of copepodids and adult *P. minutus* are not the same (Table 2). Similar observations were performed at different light harmonics. In each case, number of revolutions per minute for copepodids was higher than for adults. These differences (i.e. fast motion of mandible and first maxilla involved in the feeding currents, and low N/L and N/V ratios of second maxilla and maxillipeds involved in the capture of particles) should allow copepodids to capture small particles better than adults.

Discussion

This study illustrated the parallel changes with time occurring in the particle concentrations and in the particle food uptake by copepodids. Copepodids and adult females of *P. minutus* have an opportunis-

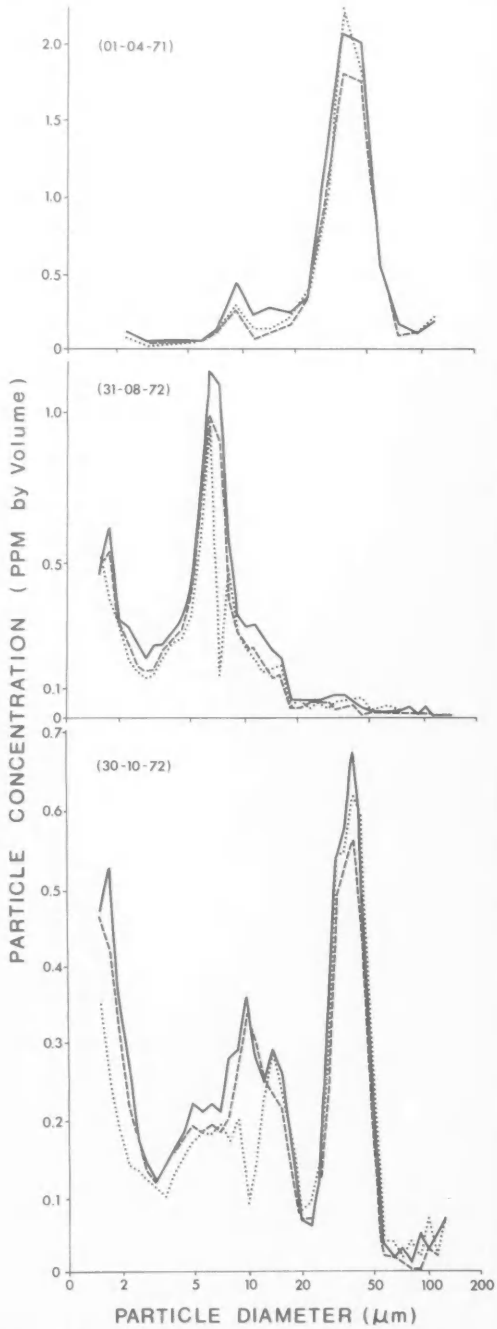

FIG. 3. Comparative feeding between copepodids (.....) and adult females (-----) of *Pseudocalanus minutus* at three different seasons. Particle size spectrum in control (——). Date of experiments is in parentheses. See method for details.

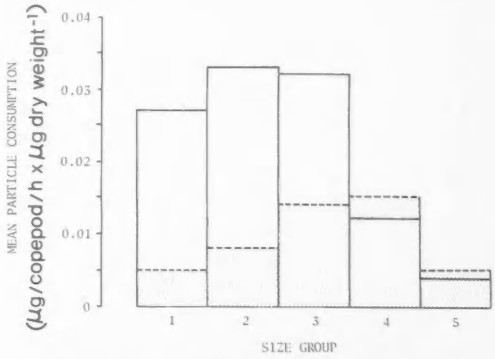

FIG. 4. Comparison of the mean consumption between copepodids (white) and adult females (stippled) of *Pseudocalanus minutus* fed simultaneously on the same particulate matter. Size-groups and time of experiments as in Fig. 1. Means are significantly different in groups 1, 2, and 3; they are not significantly different in group 4 and 5 (t-test; $P = 0.05\%$).

tic feeding behavior and can utilize the same particles within the size range 1.5–144 μm; however, adult copepods and copepodids have ingestion rates that differ sharply at the lower food-size limits (<15 μm) (Fig. 4) due to morphological characteristics of their mouthparts (Anraku and Omori 1963; Mullin 1966; Nival and Nival 1973; and Table 2). Also, their optimum food uptake does not occur at the same particle size (Fig. 4). The total quantity of particles ingested relative to copepod body weight is significantly different ($P \leq 0.05\%$) between adults and copepodids (Fig. 4). This result is consistent with the basic relationship between metabolism and size of an animal.

Similar results have been obtained with all stages of *Calanus helgolandicus* (Mullin and Brooks 1970; Paffenhöfer 1971). These results apparently contrast with more recent data which indicate that the specific ingestion rates were constant with increasing body weight of copepods (Paffenhöfer and Harris 1976; Allan et al. 1977). The discrepancy noticed among these consecutive results (Paffenhöfer and Harris 1976; and present study) is partially explained by the range of weights in *Calanus* and *Pseudocalanus* as mentioned by Paffenhöfer and Harris (1976). Another explanation relies on the sizes of the phytoplankton cells offered to the copepods in each grazing experiment. When *Calanus helgolandicus* were fed with either small-size cells (*Lauderia borealis* 19 μm diam) or with large ones (*Gymnodinium splendens*, 60 μm diam), respectively, the range of grazing rates per body weight differed widely between copepodids and adults (Fig. 5: Paffenhöfer 1971).

In a similar experiment, Paffenhöfer and Harris (1976) have fed various developmental stages of *P. elongatus* with the chain forming diatom (*Thalassiosira rotula*) the volume of which was 1×10^6

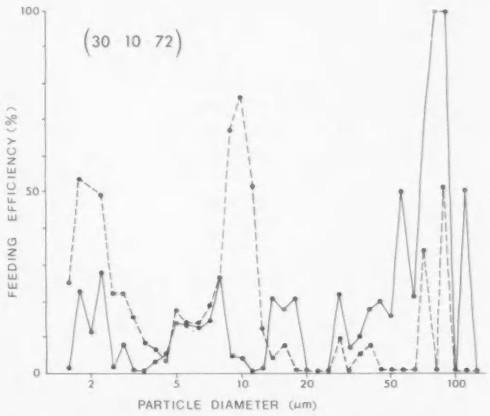

FIG. 5. Feeding efficiency of copepodids (.....) and adult females (●——●) of *Pseudocalanus minutus*. Date of experiment is in parentheses. Percent efficiency is equivalent to 100(C − G)/C, where C = particle concentration in control and G = particle concentration after grazing computed for each particle-size category.

μm^3/cell, which is equivalent to a particle size of ~114–128 μm (spherical diameter). Such cells would belong to the size-group 5, and ingestion rates per body weight are not significantly different between young and adult copepods in the particle size-groups 4 and 5 (Fig. 4), a result that agrees well with Paffenhöfer and Harris' data (1976, fig. 5). Therefore, the feeding pressure of copepodids and adults on particles are apparently significantly different only when small-size particles are involved in the food-getting process (Fig. 3, 5). These results are all in agreement with previous experiments showing that small copepods select small phytoplankton species and larger ones preferentially remove larger cells (Marshall and Orr 1955; Mullin 1963; Richman and Rogers 1969; Martin 1970; Taguchi and Fukuchi 1975).

However, results by Allan et al. (1977) showing a constant filtering rate vs. body weights do not fit the interpretation given in the above discussion. The feeding efficiency curve (Fig. 5) for each category of copepod stage varies with particle size and it gives further support to the fact that young copepods are generally more efficient consumers than adults with regard to small particles.

Young stages of copepods can play a major part in the consumption of particles due to their high grazing ingestion capability (Paffenhöfer 1971). Intraspecific competition likely takes place among different developmental stages of copepod (Fig. 3), when adults and copepodids fed simultaneously on the same particle spectra. Figure 5 shows further the selective feeding of all copepod stages on any particle categories causing the particle peaks over the spectra (Fig. 3). This active feeding mechanism is consistant with previous results on adult copepods

TABLE 2. Comparison between the mouthparts of copepodid and adult female *Pseudocalanus minutus*. N, mean sum of the total number of setae on the coxopod, basipod, and endopod of each appendage; excluding coxopod of maxillipeds; L, mean sum of the length of each of the segments excluding coxopod of maxillipeds; V, mean volume of hemisphere with diameter corresponding to L. Values ± SD's. Number of observations are in parentheses.

	Copepodid stage CIII (5)				Adult female (5)			
	Mandible	First maxilla	Second maxilla	Maxillipeds	Mandible	First maxilla	Second maxilla	Maxillipeds
N	19.6±1.3	46.2±1.9	22.6±0.9	19.8±2.4	22.7±0.5	59.4±0.5	22.0±0	27.6±0.5
L (μm)	121.4±6.7	172.5±4.6	85.0±2.5	195.5±9.0	196.2±12.4	301.1±32.9	135.1±2.9	334.0±13.7
V (μm^3)	$4.69\times10^6\pm164$	$1.34\times10^6\pm81$	$1.61\times10^5\pm69$	$1.96\times10^6\pm381$	$19.75\times10^6\pm998$	$7.15\times10^6\pm18646$	$6.45\times10^5\pm13$	$9.75\times10^6\pm1346$
Ratio N/L	0.161	0.267	0.265	0.101	0.116	0.198	0.162	0.083
Ratio N/V $\times 10^{-5}$	4.2	344.6	14.1	101.2	1.14	83.0	3.4	28.2
Relative vibration (rpm)	Stages CI, II, III 5061 ± 538 (102)				(90) 2864 ± 224 slow (53) 3557 ± 736 fast } swimming			

(Poulet 1973, 1974) and the recent work on juveniles of other copepod species (Allan et al. 1977). However, young copepods can overcome feeding competition from the adults in the particle range <10 μm because of their higher filtration capabilities for small particles (Fig. 4).

The importance of small particles in copepodid feeding seems to be fundamental and is related simultaneously to the nature, potential nutritive value, and productivity of such particles. In different geographical areas, marine particulate matter may include materials of diverse origins and may consist of different proportions of terrestrial materials, phytoplankton, algae, heterotrophic organisms, and detritus with attached bacteria (eg. Riley 1970; Parsons and Seki 1970). Living or nonliving particles constitute a potential food stock and both are utilized by copepods (Balch 1971; Heinle and Flemer 1975; Poulet 1976). Newell (1965) has shown that the nutritive value of detritus (expressed as carbon and nitrogen content) is higher in fine particles. Similarly, Mullin (1975) indicated that the 1–10 μm fraction alone of suspended matter contributed up to 58% of the total particulate organic carbon within the 1–500 μm size range. The increased surface of fine particles presents an ideal substrate for the growth of microorganisms. This rich microorganism–detritus system has great potential food value for suspension-feeders (Odum 1970). Decrease of the size of the particles in detritus tends to increase its biologically active surface (Fenchel 1970; Hargrave 1972). Recent studies on suspended matter in the St. Lawrence estuary (S. A. Poulet et al. unpublished data) indicate that during the summer over 50% of the total concentration of each organic particulate component measured in the 0.8–202 μm range (carbon, nitrogen, protein, carbohydrate, lipid, chlorophyll, and ATP) was contained in the fraction <15 μm. Sutcliffe (1972) has shown the importance and the large proportion of living material in particles <8 μm. Providing that small cell sizes have faster growth rates and higher production than larger cells (Eppley and Sloan 1966; Watt 1971; Sheldon et al. 1973), a large part of the production in seawater is likely due to small particles. The production of detritus alone, however, is more difficult to assess. As Parsons (1963) pointed out, the utilization of detritus by marine organisms will tend to increase the efficiency of the conversion of carbon.

Young copepods generally have a higher grazing and ingestion rate per unit body weight than the older stages, and they feed continuously. Their potentially higher energy requirements are likely overcome by selecting the living high-nutritive particles from the high standing stock of the nonliving fraction (Sutcliffe 1972; Poulet 1976), especially at times when the population density of copepodids and adult copepods is at a maximum. By feeding intensively on small particles, copepodids should make the major contribution to the balance in the production–predation system within the smaller particle categories. These results further suggest that rapid turnover should exist within the portion of the food web involving small particle production and the smaller copepods. The ability to partition the particulate food stock by the different development stages should be beneficial to the copepod population as a whole, in terms of feeding efficiency, utilization of a broader range of particles from those available, reduction in feeding competition, and survival of juveniles and recruitment.

Furthermore, these findings provide evidence that feeding niches are partially separated between young and adult copepods. This is of great importance in the understanding of the lower trophic levels of the marine food web where particles and copepods are the major pathways for energy flow.

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Changes in Specific Gravity of Atlantic Salmon (*Salmo salar*) Alevins

R. H. PETERSON AND J. L. METCALFE

Department of Fisheries and the Environment, Fisheries and Marine Service, Biological Station, St. Andrews, N.B. E0G 2X0

PETERSON, R. H., AND J. L. METCALFE. 1977. Changes in specific gravity of Atlantic salmon (*Salmo salar*) alevins. J. Fish. Res. Board Can. 34: 2388–2395.

The specific gravity of Atlantic salmon (*Salmo salar*) alevins decreases during posthatching development from 1.067 at hatching to 1.044 at terminal yolk resorption. The water content of the embryo is ca. 84% throughout posthatching development while that of the yolk is ca. 56%. Therefore, as the embryo grows at the expense of yolk material, the water content of the alevin increases during development. This increase in water content can entirely account for the observed change in specific gravity. Alevins reared at lower temperatures have a higher specific gravity for any given embryonic length, implying the presence of more yolk reserves. Splake alevins reared in a hatchery tray had a lower specific gravity at a given length than did alevins reared in gravel or artificial turf substrates. Measurements of specific gravity in conjunction with length measurements during development may be useful in comparing different incubation conditions.

Key words: specific gravity, Atlantic salmon, alevin, yolk, embryo, water content, temperature, splake

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Au cours du développement d'après éclosion, le poids spécifique d'alevins de saumon atlantique (*Salmo salar*) passe de 1.067 à l'éclosion à 1.044 à la résorption complète du vitellus. Le contenu en eau de l'embryon est d'environ 84% et demeure constant, alors que celui du vitellus est d'environ 56%. C'est dire qu'à mesure que l'embryon croît au dépens du matériel vitellin, le contenu en eau de l'alevin augmente durant le développement. Cette augmentation de la teneur en eau explique le changement observé dans le poids spécifique. Les alevins élevés à des températures plus basses ont un poids spécifique plus élevés, quelle que soit la longueur embryonnaire, ce qui suggère la présence de réserves vitellines supplémentaires. Les alevins de truite moulac élevés sur un plateau de pisciculture ont un poids spécifique moindre à une longueur donnée que les alevins élevés sur des substrats de gravier ou de gazon artificiel. Des mesures de poids spécifique faites en mêmes temps que les mesures de longueur au cours du développement pourraient servir à comparer différentes conditions d'incubation.

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CHANGES in the chemical constituents of salmonid eggs and alevins during yolk resorption have been documented on several occasions (Hayes and Armstrong 1942; Suyama and Ogino 1958; Ando 1962; Takama et al. 1969). These studies indicate that the water content of the alevin at hatching is 64–65%. The water content increases during yolk resorption until, at terminal yolk resorption, the fry contains 80–85% water. The water content of yolk material (Hayes and Armstrong 1942) has been found to be 59% at hatching and 55.5% at one-half yolk resorption, while the embryo (embryo, as used in this paper, is defined as the developing organism minus the yolk supply; the alevin is the embryo + yolk) was found to be 85% water. Marr (1966) estimated the yolk and embryo water contents to be 59 and 84%, respectively. The available information therefore suggests that the water contents of yolk and embryo may remain relatively constant throughout yolk resorption at 55–60% and 84–85%, respectively. Consequently, as the embryo grows at the expense of yolk material, the water content of the alevin as a whole increases.

The changes in water content during development of the alevin, therefore, may be related to conversion of a dense, dehydrated yolk material into less dense, hydrated embryonic tissue. We postulate that the specific gravity of the alevin should decrease as the amount of less dense embryonic tissue increases. Furthermore, it may be possible to relate changes in specific gravity to yolk utilization in a way that would be useful in assessing various types of incubation regimes. The results to be presented

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demonstrate the relationship between changes in specific gravity and changes in yolk and water contents of Atlantic salmon (*Salmo salar*) alevins during posthatching larval development.

Materials and Methods

The experiments were performed during the winters of 1975–76 and 1976–77, using Atlantic salmon (*Salmo salar*) eggs of Magaguadavic River, N.B., origin. The eggs were placed in black plexiglass hatching boxes (as described in Peterson et al. 1976) within 24 h of fertilization. Incubation temperatures were 4, 8, and 12 ± 0.5°C. Flow rates through the incubation boxes were 120 ± 30 ml/min, thus providing a perfusion velocity of 3.0–4.0 cm/min. Specific gravities and embryo lengths were measured every 5th, 7th, and 9th day after hatching at 4, 8, and 12°C, respectively, with measurements continuing until yolk resorption was over 80%. Alevins incubated at 8°C were analyzed for wet and dry weights and lipid contents of whole alevins, embryos, and yolk sacs at 2, 13, 23, 31, and 38 days posthatch. Those from the 4°C temperature were analyzed at 0, 26, 55, and 64 days.

Specific gravities were measured at 15°C by a glycerol flotation procedure. Alevins were removed from the incubation box and placed in a MS-222® solution at 15°C, thus attaining temperature equilibration during anesthesia (about 2 min). The alevins were then pipetted singly on paper toweling to remove excess water, and dropped into a 150-ml, wide-mouth jar about half filled with a glycerol solution of the required specific gravity. Only one alevin was tested per jar. Ten alevins were tested at each glycerol concentration. Care was required at this stage to ensure that the alevin surface did not dry. Otherwise, air bubbles often attached to the alevin surface and the result had to be discarded. Alevins gain or lose water rapidly when placed in the solution, so the observations must be made quickly (within 5 s), particularly at near neutral buoyancy. When first dropped into the solution, the momentum of the alevin causes it to sink. (It is better to drop it in from 2 to 3 cm height, otherwise it may adhere to the surface film in solutions of near-neutral buoyancy.) If the specific gravity of the alevin is greater than that of the solution, it will continue to sink to the bottom. If the alevin is of lower specific gravity than the solution, it will reverse direction and tend to float. At solutions of specific gravity only slightly greater than that of the alevin, the latter would begin to float, then reverse direction and sink as water was lost to the solution. At neutral specific gravity the alevin would be suspended in midsolution with no vertical movement until sufficient water were lost to make it sink. The change in alevin response from solutions of lower to those of greater specific gravity was sharp (Fig. 1). The response changed from 100% sinking to 100% floating over a range of about 0.005 specific gravity units and was therefore an accurate estimate of specific gravity. In practice the complete curve, as shown in Fig. 1, was usually not determined, as the specific gravity of neutral buoyancy (taken here to be the specific gravity at which 50% float) was very nearly known prior to determination. In such cases only two or three solutions whose specific gravities closely bracketed (±0.001) that of the alevin were tested, and the alevin specific gravity determined by interpolation.

The specific gravity of all glycerol solutions used was determined with a hydrometer with a least count of ±0.0005 immediately before use. Solutions were made more or less dense by addition of a stock solution (2 parts freshwater: 1 part glycerol) or freshwater, respectively. All solutions were kept at 15°C. The glycerol stock solution kept indefinitely, but the more dilute test solutions became contaminated with bacteria in time and had to be replaced.

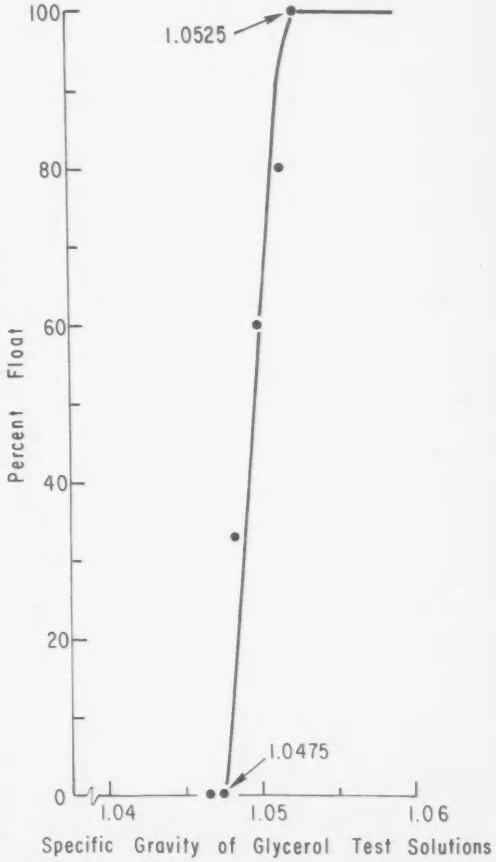

FIG. 1. Percentage of Atlantic salmon alevins that float plotted against the specific gravity of the test solution. Ten alevins were used at each specific gravity. Alevin specific gravity is taken as that of the glycerol solution in which 50% float.

For water and lipid analyses of yolks and embryos, yolk sacs were dissected with fine scissors. A small cut was made where the sac attached to the embryo posteriorly. The entire sac could then be stripped off as a unit by pulling it gently toward the anterior of the alevin with the points of the scissors. During this procedure the embryo was held by the tail with forceps, head downward, over an aluminum weighing pan. The dissected yolk sac fell onto the weighing pan. The embryo was then placed in a separate weighing pan. Three alevins, embryos, or yolks were pooled for wet and dry weight determinations. Duplicates were performed

for each determination; differences between duplicates were never more than 5% and usually much less. There was a loss of material of about 7% during dissection.

Lipids were extracted from alevins, embryos, or yolks by the chloroform–methanol extraction method of Folch et al. (1957). The chloroform extracts were dried to constant weight in a sample concentrator under vacuum at 45°C. Five alevins, embryos, or yolks were pooled for lipid analysis.

The possible presence of air in alevins was tested using a Cartesian diver technique. The method is based on the principle that, with continued expansion of gas as the pressure is lowered, the density of the organism decreases until it floats (Saunders 1965). Groups of five alevins were anesthetized in a 100-ml flask that had a ground glass connection leading to a mercury manometer–vacuum pump assembly (Saunders 1965). The water in the flask was partially degassed to prevent bubble formation upon evacuation. The flask was immersed in a constant temperature bath at 15°C.

Total volumes of yolks, embryos, and alevins at various times after hatching were determined by using the experimentally determined values of wet weights and specific gravities (sp gr) and the equation, vol = (wet wt)/(sp gr). Volumes of nonaqueous components of alevins, embryos, and yolks were determined by subtracting the water volumes from the total volumes.

Results and Discussion

As postulated in the introduction, the specific gravity of Atlantic salmon alevins decreased throughout development (Fig. 2). The specific gravity of newly hatched alevins was 1.0660–1.0675 for all incubation temperatures, and it declined to 1.0460–1.0470 near the end of the experiment. The specific gravity declined more rapidly at higher incubation temperatures. Bonham (1976) determined the specific gravity of rainbow trout (*S. gairdneri*) eggs to be 1.076 prior to water hardening and 1.064 after water hardening. This latter value is slightly lower than that for newly hatched Atlantic salmon alevins. Since the watery perivitelline space is lost upon hatching, the newly hatched alevin may have a higher specific gravity than does the egg. The specific gravity might decrease due to increased water content, but two other phenomena could occur during alevin development that might, at least partially, produce the above changes in specific gravity. Firstly, the swim bladder could be filling gradually. Secondly, the specific gravity of the nonaqueous components of the alevin might decrease during development — for example, the lipid content might increase.

No alevins between 21.2 and 27.1 mm were buoyant or floated when subjected to reduced pressures as low as 40 mm Hg (0.053 atm). Late-stage alevins were dissected to examine the swim bladder for presence of air, and none was detected. Occasionally, late-stage alevins may be found with a gas bubble in the gut, but none of the alevins tested in these experiments was so afflicted. Fry (at the termination of yolk resorption) do ingest air (Tait 1960), and this process occasionally dictated the termination of an experiment.

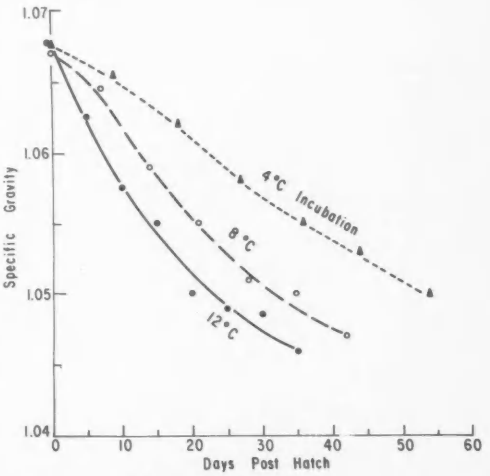

FIG. 2. Specific gravities of Atlantic salmon alevins as a function of time after hatching for three incubation temperatures.

Lipid content decreases during development of the alevin, at least on a wet weight basis (Suyama and Ogino 1958; Phillips and Dumas 1959; Ando 1962; Takama et al. 1969). Similar results were obtained here with the percent lipid declining from 8.2 at hatching to 4.0 near completion of yolk resorption. On a dry-weight basis, the lipid content increased by about 1% (NS) for the first 23 days of development at 8°C, then decreased by 4% over the last 16 days (Fig. 3A). It would seem that the observed changes in specific gravity with development cannot be accounted for, even in part, by change in lipid content.

The decrease in specific gravity with development is, however, closely correlated with an increase in water content of the whole alevin (Fig. 3B). An analysis of the water content of dissected yolks and embryos (Table 1) indicates that the water content remains nearly constant throughout development at 56 and 84% (weight basis), respectively. There is a suggestion that the water content of the yolk may rise slightly, and that of the embryo decrease slightly, near the end of development. These values for water content of embryo and yolk agree with those cited in the literature (Hayes and Armstrong 1942; Marr 1966). Owing to conversion of yolk to embryo, the alevin water content increases steadily during development from 66% at hatching to 83% at complete yolk resorption. Suyama and Ogino (1958) and Ando (1962) found values of 59% H_2O at hatching, and 80–84%, respectively, at swim-up for rainbow trout (*S. gairdneri*) alevins. The measured water

TABLE 1. The calculated water content of Atlantic salmon alevins as derived from water content of dissected embryos and yolk sacs compared with water contents of alevins as measured directly. Water content expressed as percent total wet weight. Duplicate determinations were made, each from three to five pooled alevins, yolks, or embryos.

	% H_2O			
Days posthatch	Yolk	Embryo	Alevin (calculated)	Alevin (measured)
2	55.4, 55.1	86.2, 83.7	66.4	67.1, 66.4
13	56.9, 54.9	84.1, 86.8	72.0	73.0, 75.2
23	53.8, 54.0	83.6, 84.4	76.9	75.7, 79.2
31	57.5, 59.1	83.9, 83.9	79.3	78.5, 79.4
38	59.4, 52.2	82.3, 83.2	81.3	80.5, 80.2

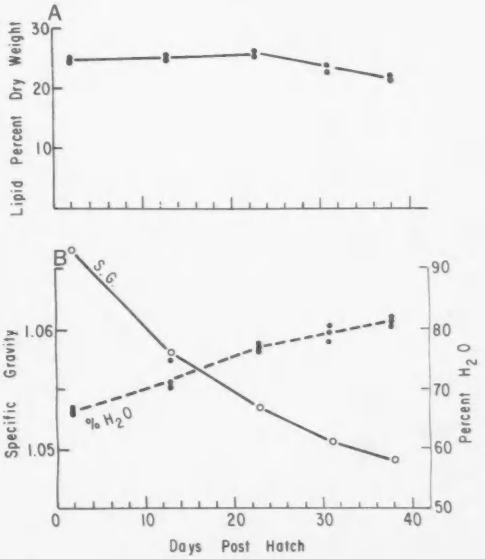

FIG. 3. A, Alevin lipid content (percent of dry alevin weight) plotted against time after hatching. B, Specific gravity (closed circles) and water content (open circles) of Atlantic salmon alevins plotted against time after hatching.

content of intact alevins agreed well with estimates of alevin water content, calculated on the basis of water content and wet weights of yolks and embryos at equivalent development times (Table 1). This indicates that no significant amounts of water evaporated during dissection.

Specific gravities of dissected embryos and yolks were measured on three occasions (Table 2). The means for embryos and yolks were 1.0440 and 1.0820, respectively. These values were used to calculate estimates of the specific gravity of the whole alevin at various development times (Table 3). These estimates agreed closely with the measured specific gravity of the intact alevin at the equivalent

TABLE 2. The specific gravity (sp gr) of dissected embryos and yolk sacs shown for various stages of development. Incubation temperature in parentheses.

Days posthatch	Embryonic length	Embryo sp gr	Yolk sp gr
5 (4°C)	19.3	1.0435	1.0800
18 (8°C)	23.7	1.0445	not measured
25 (8°C)	25.1	1.0435	1.0840

period of development (Table 3). The measured changes in specific gravity of the alevin could be entirely accounted for by the changes in relative amounts of yolk and embryo associated with the alevin's development. The specific gravity declines with development because the amount of less dense embryonic tissue increases relative to the denser yolk material.

The specific gravity of the alevin depends on the relative proportions of embryo and yolk (Table 3). Therefore the specific gravity would be expected to decrease linearly as the ratio of wet embryo weight:wet alevin weight increases (Fig. 4). The specific gravity of the embryo was determined to be 1.0440 (Table 2). The line relating specific gravity to the above ratio should therefore pass through the coordinates (sp gr = 1.0440, (embryo)/(alevin) × 100 = 100). This is the point where yolk is completely resorbed. The calculated value of specific gravity from the regression equation is 1.0452. The embryo increases in wet weight by about 18% relative to the wet weight of the alevin for each 0.005 decrease in specific gravity.

The possibility remains that changes in specific gravity of nonaqueous components other than lipids are contributing in some way to the observed changes in alevin specific gravity. The overall specific gravity of nonaqueous components (lipids + solids) in yolk material was 1.206, and remained relatively constant throughout yolk resorption (Table 4). Mean embryo nonaqueous specific gravity throughout yolk resorption was 1.364, but tended

TABLE 3. Specific gravities for alevins at various times after hatching measured directly and calculated using the proportions of yolk and embryo comprising the alevin. Yolk specific gravity of 1.0820 and embryo specific gravity of 1.0440 were used in the calculations. For example, if the alevin were 50% embryo, then the alevin specific gravity would be (1.0440)/(2) + (1.0820)/(2) = 1.0630. Incubation temperatures in parentheses. Embryos and yolks were dissected from two groups of three alevins each; embryos and yolks from each group were pooled and weighed.

Days posthatch	% of alevin that is embryo	Calculated sp gr		Measured sp gr
2 (8°C)	39.05	1.0672	1.0669	1.0665
	40.53	1.0666		
13 (8°C)	59.32	1.0595	1.0586	1.0580
	63.77	1.0578		
23 (8°C)	74.34	1.0537	1.0528	1.0535
	79.10	1.0519		
31 (8°C)	78.54	1.0522	1.0510	1.0505
	84.52	1.0499		
38 (8°C)	92.49	1.0469	1.0474	1.0490
	90.01	1.0478		
1 (4°C)	41.04	1.0664	1.0666	1.0670
	39.98	1.0668		
26 (4°C)	66.74	1.0567	1.0573	1.0580
	63.43	1.0579		

TABLE 4. The water volume (vol H_2O), nonaqueous volume (vol non-H_2O), dry weights, total specific gravities, and specific gravities of the nonaqueous components for yolks, embryos, and alevins at various times after hatching. Specific gravity of water was assumed to be 1.0. Total volume was estimated from the wet weights and the total specific gravity (vol = (wet wt)/(sp gr). The vol non-H_2O was obtained by subtraction. Non-H_2O sp gr = (dry wt)/(vol non-H_2O). Each value is the mean of determinations made on three pooled yolks, embryos, or alevins, but are expressed on the basis of a single yolk, embryo, or alevin.

Days posthatch	Vol H_2O (μl)	Vol non-H_2O (μl)	Dry wt (mg)	Total sp gr	non-H_2O sp gr
Yolk					
2	33.2	22.3	26.9	1.082	1.206
13	23.8	15.4	18.7	"	1.214
23	13.8	10.0	11.8	"	1.180
31	13.6	8.0	9.8	"	1.225
38	6.7	4.5	5.4	"	1.200
Embryo					$\bar{x}$ = 1.206
2	33.6	4.3	5.9	1.044	1.372
13	58.2	6.9	9.8	"	1.420
23	70.9	9.9	13.5	"	1.364
31	87.4	12.4	16.8	"	1.355
38	104.6	16.6	21.8	"	1.313
Alevin					$\bar{x}$ = 1.364
2	63.5	26.2	32.1	1.0665	1.225
13	82.7	25.8	32.1	1.0580	1.244
23	94.5	22.3	28.4	1.0535	1.274
31	116.7	23.3	30.4	1.0505	1.304
38	110.2	19.1	25.4	1.0490	1.330

to decrease during the later stages of the process. The lower specific gravity of nonaqueous yolk components is probably due to the fact that yolk dry weight is 34% lipid which is of low specific gravity (slightly less than 1.0). Embryonic dry weight by comparison is 17% lipid. Alevin nonaqueous specific gravity increased throughout yolk resorption, because embryonic mass was increasing and yolk mass decreasing. The decrease in total specific gravity of the alevin during yolk resorption cannot be

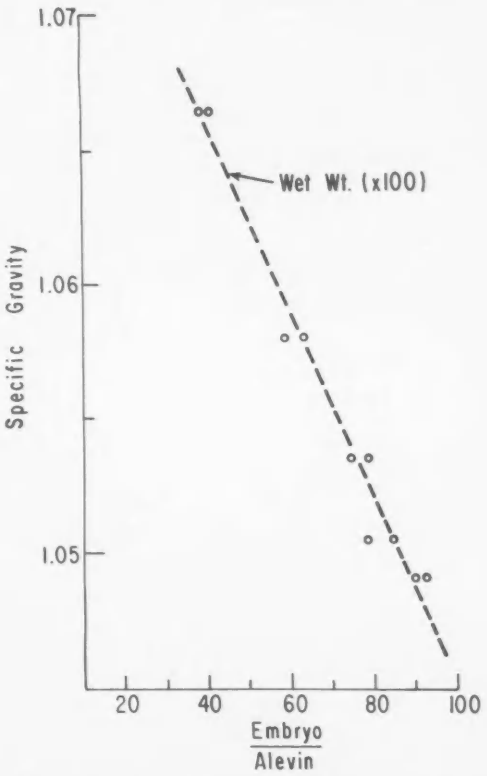

FIG. 4. Specific gravity of Atlantic salmon alevins as a function of the ratio of embryo weight:alevin weight (expressed as a percentage). The equation of best fit relating s.g. to the wet weight ratios is: sp gr = 1.0796 − 0.000344 *r*.

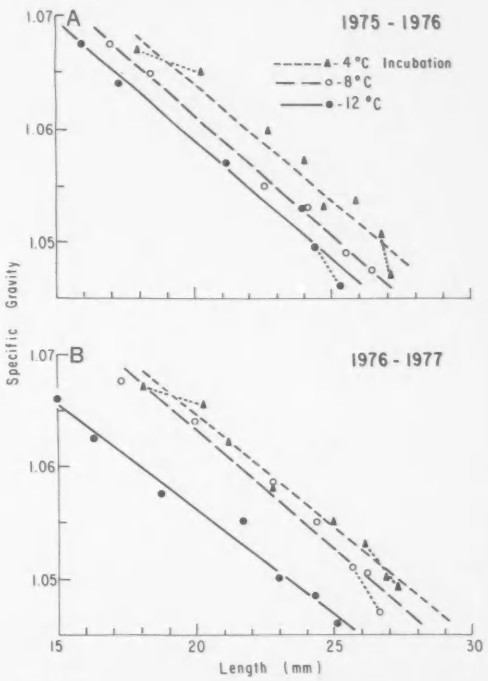

FIG. 5. Specific gravities of Atlantic salmon alevins are shown as a function of embryonic length for three incubation temperatures. A, Measurements made in 1975–76; B, measurements made in 1976–77. Regression equations: 1975–76: 4°C, sp gr = 1.1069 − 0.00212 L: 8°C, sp gr = 1.1044 − 0.00215 L: 12°C, sp gr = 1.1010 − 0.00209 L. 1976–77: 4°C, sp gr = 1.1034 − 0.0196 L: 8°C, sp gr = 1.1055 − 0.00212 L: 12°C, sp gr = 1.0934 − 0.001867 L.

explained by, and indeed runs counter to, the specific gravity changes of the nonaqueous components of the alevin.

It has been shown above that changes in specific gravity are related to changes in the proportions of embryonic and yolk tissue which compose the alevin. Therefore, measurement of specific gravity in conjunction with some measure of embryo size should yield an estimate of growth efficiency which can be compared, on a relative basis, among different groups of alevins. Let us assume, as an example, that we have two groups of alevins from a single batch of eggs. These two groups have been reared under different incubation regimes, such that one group has grown more efficiently. If they have the same embryonic size, then the group that has grown most efficiently will have more yolk remaining and therefore a higher specific gravity. Two examples of such comparisons follow:

Alevins reared from fertilization to complete yolk resorption at lower temperatures are larger than those so reared at higher temperatures (Gray 1929; Peterson et al. 1976; Hamor and Garside 1976). The specific gravities of alevins reared at 4, 8, and 12°C in two different years are plotted vs. their corresponding lengths (Fig. 5). Alevins reared at lower temperatures have higher specific gravities at a given embryonic length. For example in Fig. 5B (1976–77 data), alevins reared to an embryonic length of 23 mm had a specific gravity of 1.0500 at 12°C, 1.0570 at 8°C, and 1.0590 at 4°C.

There are several points of interest in Fig. 5. Firstly, the specific gravities of hatching are nearly constant at 1.0660–1.0675 over the range of temperatures investigated, although alevins incubated at 4°C hatch at 3 mm longer than those incubated at 12°C. Secondly, the slopes of the lines relating specific gravity to embryonic length do not differ significantly among the alevins at various incubation temperatures for either year. Thirdly, the specific gravity often changes rapidly over the last millimetre or so of length increase (indicated by dotted lines at 8°C in 1976–77 and at 4 and 12°C in 1975–76).

The constancy of the specific gravity of newly

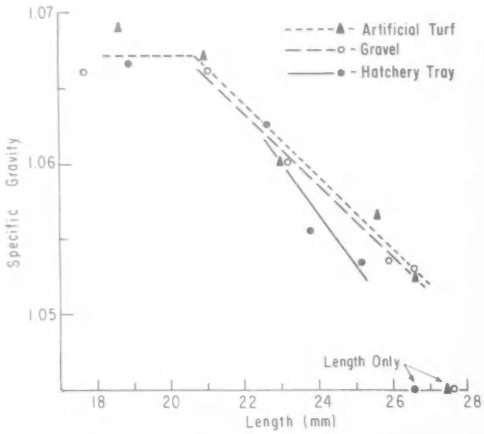

FIG. 6. Specific gravity of splake (*Salvelinus namaycush* × *S. fontinalis*) alevins against embryonic length. The three groups of alevins were reared under differing incubation conditions as indicated. Regression equations of best fit are: gravel substrate, sp gr = 1.1155 − 0.00238 L; artificial turf, sp gr = 1.1153 − 0.00234 L; hatchery tray, sp gr = 1.1384 − 0.00340 L. Points indicated by arrows are lengths at which alevins began to take air into swim bladder.

hatched alevins at various incubation temperatures, coupled with larger alevin size at lower temperatures (Fig. 5), implies more efficient use of yolk material at lower temperatures prior to hatching. On the other hand, the similarity of the slopes relating specific gravity to length during yolk resorption after hatching suggests that the efficiency of yolk utilization is similar at all posthatching temperatures. Atlantic salmon alevins have been observed by others to grow more efficiently at the higher temperatures (Marr 1966; Hayes and Pelluet 1945). The changes in specific gravity described here cannot be directly related in any simple way to absolute conversion efficiency of yolk to embryo, because efficiency is necessarily based upon dry weights. Using the method of Marr (1966) the gross conversion efficiency of the 8°C alevins used in these experiments was determined to be 0.71. Marr calculated gross conversion efficiencies of 0.70 at 10°C and 0.65 at 7.6°C for Atlantic salmon alevins. The use of specific gravity and length measurements does appear to have possible utility to compare relative growth efficiencies of alevins. The method has the advantage of being quick, simple, and obviates the necessity of killing alevins. It may also be of use in separating groups of faster and slower developing alevins.

The increased slope of specific gravity vs. length toward the end of yolk resorption (Fig. 5) may mean that growth during this period involves proportionately greater increase in mass relative to increase in length. Alternatively, it could mean that the alevins use more energy for locomotor activity at this point.

During the winter of 1976–77, several groups of splake (*Salvelinus namaycush* ♀ × *S. fontinalis* ♂) eyed eggs were placed on three different substrates for incubation until yolk resorption. These substrates were (1) an incubation box with a layer of gravel in the bottom, (2) an incubation box containing several layers of artificial turf material, and (3) a standard stainless steel incubation tray with perforated bottom. The specific gravities of alevins reared in all three conditions were similar up to a length of about 23 mm (Fig. 6). Beyond this point the specific gravities of alevins reared in the hatchery tray was lower than that of alevins in the other incubation media at equivalent lengths. The length at the stage when air was taken into the swim bladder was less for alevins reared in the hatchery tray (Fig. 6). The hatchery alevins were significantly shorter ($t = 3.17$, $P < 0.01$).

The mean wet weights for three groups of five pooled alevins at the end of the experiment were 119.7, 126.6, and 129.3 mg for alevins from hatchery, gravel, and artificial turf substrates, respectively. The corresponding dry weights were 23.2, 24.0, and 24.3 mg, respectively. Thus the alevins reared in the hatchery tray were not smaller due to slower development — hence more yolk. Such a situation should result in heavier alevins, not lighter. The incubation temperatures were 7.4, 7.8, and 7.8 ± 0.7°C for hatchery tray, gravel, and artificial turf, respectively, and cannot account for the difference in size. Locomotor activity of alevins "competes" with growth for energy stored in the yolk. Consequently, incubation conditions leading to excessive activity may result in smaller alevins, as in Fig. 6 (also Marr 1963, 1965). In some commercial hatchery trays it has been noted that alevins are continually active, while with a bottom material (gravel, grooved bottom, etc.) they are more quiescent. Whether the locomotor activity possibly confers advantages that offset smaller size has not been considered. It should be pointed out that the particular artificial turf preparation used here is not a desirable incubation medium. The edges of the plastic were sharp, resulting in lacerated and punctured yolk sacs and subsequent death in 47% of the alevins reared in this medium. Mortality in the gravel medium was 18%.

Acknowledgments

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Migrations and Activity Levels of Overwintering Atlantic Herring (*Clupea harengus harengus*) along Southwest Newfoundland

G. H. WINTERS

Department of Fisheries and the Environment, Fisheries and Marine Service, Research and Resource Services, Newfoundland Region, St. John's, Nfld. A1C 1A1

WINTERS, G. H. 1977. Migrations and activity levels of overwintering Atlantic herring (*Clupea harengus harengus*) along southwest Newfoundland. J. Fish. Res. Board Can. 34: 2396–2401.

Recoveries of tagged Atlantic herring (*Clupea harengus harengus*) released with abdominally inserted magnetic tags indicated a rapid and random dispersion of tagged fish within the total population of herring along southwest Newfoundland. Recoveries further indicated a general westward movement of herring along southwestern Newfoundland from January to March, also reflected in the spatial distribution of commercial catches during this period. Metabolic rates of these overwintering herring, estimated from changes in body energy from December to March, were more than double the standard level, suggesting a high degree of activity, possibly due to avoidance behavior in relation to predatory actions by cod overwintering in the same area.

Key words: tagging, movements, predation, metabolic levels

WINTERS, G. H. 1977. Migrations and activity levels of overwintering Atlantic herring (*Clupea harengus harengus*) along southwest Newfoundland. J. Fish. Res. Board Can. 34: 2396–2401.

Les recaptures de harengs atlantique (*Clupea harengus harengus*) marqués avec marques magnétiques insérées dans l'abdomen indiquent une dispersion rapide et au hasard des poissons marqués parmi la population entière de harengs le long de la côte sud-ouest de Terre-Neuve. Les recaptures indiquent de plus un mouvement général vers l'ouest le long de cette côte de janvier à mars. La répartition spatiale des prises commerciales durant cette période réflète cette migration. Les taux métaboliques des harengs hivernant dans cette région, estimés à partir des changements dans l'énergie corporelle entre décembre et mars, sont plus du double du niveau normal. Ceci donne à croire qu'il y a un haut degré d'activité, probablement causé par un comportement d'évitement suscité par l'action prédatrice de la morue franche qui hiverne dans la même région.

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TAGGING experiments (Winters and Beckett 1977) and comparisons of biological characteristics (Hodder and Parsons 1971) have demonstrated that herring that overwinter along southwest Newfoundland (Fig. 1) are derived from a stock complex of herring that spawn and feed in the southern Gulf of St. Lawrence and emigrate from that area in late fall. There is, however, very little information available on the small-scale migrations of overwintering herring along southwest Newfoundland and whether such movements are active or mainly passive. The nature of the tagging experiments conducted along southwest Newfoundland (abdominally inserted metallic tags recovered from bulk landings by magnetic separators in reduction plants) precluded detailed analyses of local movements during the overwintering period. However, in January 1971 an electronic tag detection system capable of monitoring the landings of each vessel was installed in the reduction plant at Isle aux Morts, Newfoundland, immediately following a herring tagging experiment in Bay de Loup (Fig. 1) and continued to monitor landings at scheduled daily periods until late March 1971. This report analyzes these detailed tag recoveries as well as ancillary data relating to local movements of overwintering herring along southwest Newfoundland.

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Methods and Materials

During January 25–26, 1976, 10,000 herring with abdominally inserted ferro-magnetic tags (Winters and Beckett 1977) were released in the Bay de Loup area (Fig. 1). Length, sex, and maturity data were obtained from samples of the fish used in the tagging experiment, as well as information on surface temperatures, fish conditions, and presence of predators. Tagged fish recovered by the electronic tag detector were measured, weighed, appropriately identified, and frozen for more detailed examination at the Newfoundland Biological Station, St. John's. Area of capture and other relevant catch information was obtained simultaneously from the weight-master or directly from the

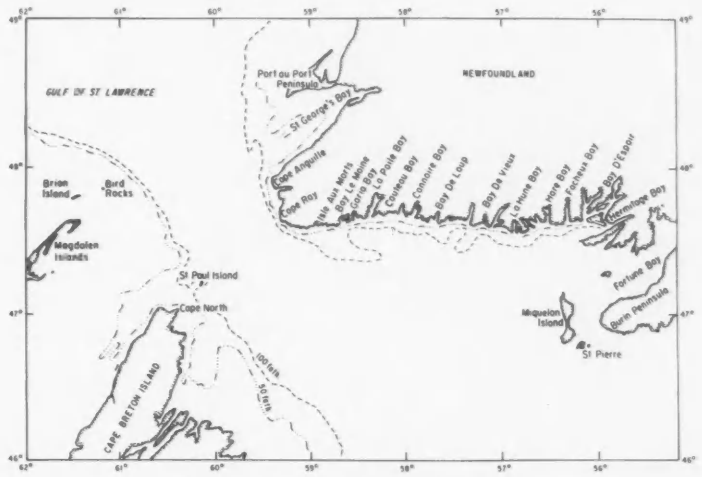

FIG. 1. Locations mentioned in text.

vessel's skipper. The detection unit was calibrated for recovery efficiency each day until an efficiency of at least 90% was achieved.

Results

COMPARISON OF RELEASED AND RECAPTURED FISH

Mean length of spring- and fall-spawning herring tagged and released at Bay de Loup in January 1971 were very similar to length of tagged fish from the same experiment recaptured during the February–March period along southwest Newfoundland. No significant differences were evident in the relative percentage of spring- and autumn-spawners (Table 1) in the recaptured fish compared to the released fish, whereas the sex ratio of the recaptured fish was significantly different in favor of the females. Because of the small number of recaptured fish involved in the comparison it is questionable whether such a difference represents differential tagging mortality.

The above results thus suggest that, at least in the period immediately following tagging, the fishery was evenly distributed on the tagged population.

DISPERSION CHARACTERISTICS OF THE TAGGED HERRING

A total of 6288 t of herring representing 63 separate landings were scanned by the electronic tag detector; the tag recoveries are listed by weekly period and tagging experiment (Winters and Beckett 1977) in Table 2 and in relation to distance from the tagging site for the Bay de Loup experiment in Table 3. The relative proportion of tag recoveries from the various releases is similar to that documented by Winters and Beckett (1977) for the total tag returns during the same period, i.e. highest recoveries from the Bay de Loup releases and lowest from the Magdalen releases.

TABLE 1. Comparison of average lengths (mm) and % males (in parentheses) of released and recaptured herring from the Bay de Loup tagging experiment; % spring was 22.5 at release and 27.7 at recapture

Type	Released	Recaptured
Spring	337 (55.6)	335 (46.2)
Autumn	351 (50.3)	341 (41.2)
Combined	348 (51.5)	345 (42.6)

Temporal and spatial variations in the distribution of tagged herring within the total population have been evaluated by plotting the number of tags recovered per 1000 tonnes landed against time after release (Fig. 2A) and distance from the release area (Fig. 2B) for the Bay de Loup tagging experiment. Regression analyses result in nonsignificant correlations between the respective variables suggesting an immediate diffusion of the tagged fish within the exploited population and that such diffusion occurred without a differential migration rate with respect to distance.

A further test of the random distribution of tagged fish within the exploited population of herring along southwest Newfoundland may be obtained from the distribution of the number of tags per landing for the Bay de Loup releases. The data are given below:

No. tags per landing	No. of landings
0	28
1	14
2	10
3	3
4	1

TABLE 2. Weekly tag recoveries in southwest Newfoundland during 1971 by the electronic tag detector.

Date 1971	Tag recoveries by area of release: La Poile–Rôti bays, 1970	Magdalens 1970	Gaspé 1970	Bay de Loup 1971	Total tags recovered	No. of landings scanned	Vol of landings scanned (t)
Jan. 27–Feb. 2			4	8	12	7	1110
Feb. 3–Feb. 9			1	5	6	13	1094
Feb. 10–Feb. 16						1	175
Feb. 17–Feb. 23	3		2	18	23	11	1500
Feb. 24–Mar. 3	1	1	1	6	9	13	958
Mar. 4–Mar. 10			3	1	4	3	218
Mar. 11–Mar. 17	1		8	7	16	7	874
Mar. 18–Mar. 24			1	2	3	6	309
Mar. 25–Apr. 1						2	50
Total	5	1	20	47	73	63	6288

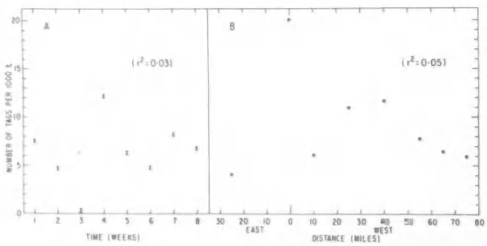

FIG. 2. Relationship between number of tags recovered by electronic tag detector per 1000 t landed and (A) time after release and (B) distance from the tagging site (naut. miles).

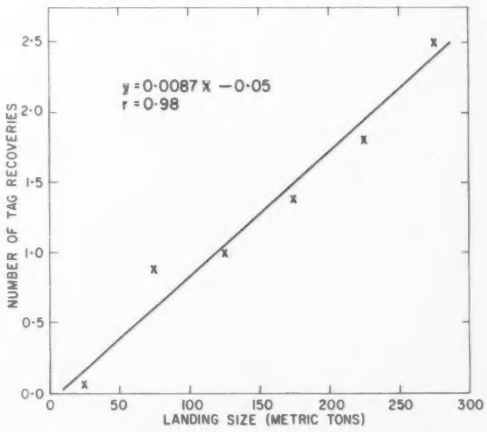

FIG. 3. Relationship between number of tags of Bay de Loup experiment recovered by electronic tag detector and landing size.

Since vessel landings were not of equal size, a Poisson test of random dispersion of tagged fish was not possible. However, if the distribution of different sizes of catches is relatively uniform over the areas of capture, then information on the effectiveness of tag dispersion can be obtained from comparison of tag recoveries with catch size. Inspection of catch sizes along southwest Newfoundland in 1971 (data on file at the Newfoundland Biological Station) indicates no differences among bays or times within bays. Accordingly, the relationship between the number of tags of the Bay de Loup experiment recovered per landing by the electronic tag detector and catch size was determined by regression analyses (Fig. 3). The apparent linearity of the relationship is verified by the high coefficient of determination ($r^2 = 0.96$). We may safely conclude that the tagged fish released at Bay de Loup in January 1971 were randomly distributed throughout the exploited population.

LOCAL MIGRATIONS ALONG SOUTHWEST NEWFOUNDLAND

During the 1st-wk after release some tagged herring from the Bay de Loup tagging experiment had moved as far west as Garia Bay, a distance of 65 naut. miles (Table 3). However, even up to a month after tagging some tagged fish were still present in the tagging locality. Only a single tag was recovered in 1971 by the electronic tag detector from catches made east of Bay de Loup where the catches and the number of tags recovered per 1000 tonnes scanned were at low levels. The remainder of the tags were recovered from landings of catches made west of the tagging locality. To evaluate the net migration pattern indicated by the tag recoveries, a regression of mean distance traveled westwards against time after release has been carried out (Fig. 4). The correlation coefficient is significant ($P < 0.05$), thus suggesting a general westward migration of herring along southwest Newfoundland during the winter season.

The spatial distribution of seiner catches along southwest Newfoundland in 1971 (Fig. 5) supports the general westward migration of herring shown by tag recaptures. Herring arrived from the southern

TABLE 3. Tag recoveries by the electronic tag detector from the Bay de Loup tagging experiment by area of catch and weekly period (E = East, W = West).

Recapture area	Distance from tagging area (naut. miles)	Tag recoveries/1000 t scanned during wk no.								Total recoveries	Total catch (t)
		1	2	3	4	5	6	7	8		
Bay de Vieux	25 E	4.0								1	250
Bay de Loup	0				20.0					2	100
Barachois Bay	10 W		6.0							1	166
Connoire Bay	25 W				10.9					2	184
Couteau, Cinq Cerf bays	40 W	16.2			14.6	10.4		2.1		20	1800
Rôti; La Poile bays	55 W		3.5		10.5			14.3		12	1563
Garia Bay	65 W	19.7	4.3		17.5	1.7	7.3			7	1174
Bay le Moine	75 W					5.6			5.7	2	354
Total		39.9	13.8	—	73.5	17.7	7.3	16.4	5.7	47	5591
Mean distance traveled (naut. miles)		46 W	39 W	—	36 W	54 W	65 W	53 W	75 W		

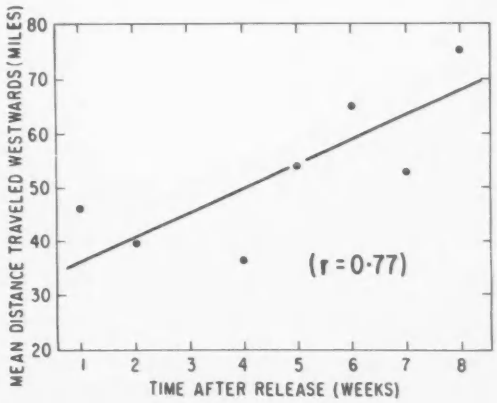

FIG. 4. Relationship between mean distance traveled westwards (naut. miles) and duration of release of tagged fish released at Bay de Loup, January 1971.

Gulf in late November 1970, and by December were widely distributed in the fjords mainly east of Burgeo. After December the fishery gradually shifted westwards and the last catches for the season were made in April off the southwest corner of Newfoundland from La Poile Bay to Rose Blanche. A similar westward shift in the fishery was observed beginning in February in 1969 (Hodder 1969).

ACTIVITY LEVELS DURING OVERWINTERING

The type of migration pattern, either active or passive, that causes the change in distribution patterns of overwintering herring along southwest Newfoundland should be reflected in the activity level of the fish, i.e. actively migrating herring should be characterized by a metabolic level close to the normal for that temperature, whereas passively migrating herring should have a metabolic level close to the standard level. Since these overwintering herring do not feed (Parsons and Hodder 1975), all energy expenditures during this period must originate from body sources, thereby causing a loss in body weight, which when expressed in energetic equivalents, can be used to calculate metabolic levels. Monthly length–weight data and proximate composition data for the 1970–71 winter fishery are available from Hodder et al. (1972, 1973). Fish in the modal length of each spawning group (spring and fall) have been taken as representative of that component, and their weight loss from mid-December 1970 to mid-March 1971 has been expressed in terms of millilitres O_2 per gram per hour using the proximate caloric (1 g fat = 9500 cal; 1 g solid = 5000 cal) and oxycaloric (1 ml O_2 = 4.86 cal) equivalents (Table 4). Comparison of these values with the standard metabolic level (Table 4) calculated at 3°C from $Q = 0.3\,W^{0.8}$ (Winberg 1956) and the appropriate Krogh conversion factor suggests that the metabolic level of overwintering herring along southwest Newfoundland is apparently substantially greater than the standard level. Since for most fish the basal metabolic level is approximately 60% of the standard level (Winberg 1956), we may conclude that the overwintering migrations of herring along southwest Newfoundland are characterized by movements of fish in a high state of activity. This agrees well with the information gathered from tag recoveries and also with our observations on the lively condition of the herring used in the tagging experiments.

Discussions and Conclusions

Tag recoveries by the electronic tag detector show that there is some eastward as well as west-

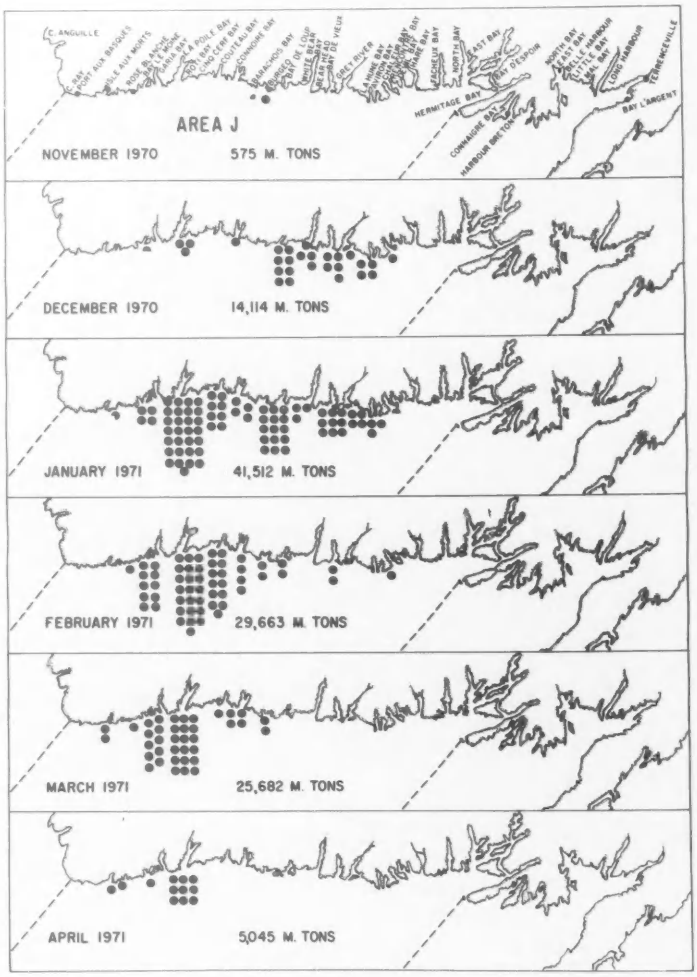

FIG. 5. Spatial distribution of monthly seiner catches along southwest Newfoundland in 1971.

TABLE 4. Calculation of activity levels of spring- and fall-spawning herring along southwest Newfoundland from energy loss during December 10, 1970–March 4–21, 1971 (90 days). Weights at modal lengths (335 mm for springs and 350 mm for autumns) were obtained from Hodder et al. (1972) and fat content data from Hodder et al. (1973); standard metabolism at 3°C has been calculated from $Q = 0.3W^{0.8}$ and Krogh conversion factor (Winberg 1956).

Spawning group	Wt (g) at modal length		Proximate composition (g)										Calc. std. met. rate at 3°C (mg $O_2 \cdot g^{-1} \cdot h^{-1}$)
			Dec. 10, 1970				Mar. 4–21, 1971						
	Dec.	Mar.	Fat	Solid	Water	Energy content (kcal)	Fat	Solid	Water	Energy content (kcal)	Energy loss (kcal)	Oxycaloric equivalent (mg $O_2 \cdot g^{-1} \cdot h^{-1}$)	
Spring	316	298	54.1	60.0	201.9	814.0	46.3	51.1	200.6	695.4	118.6	.034	.015
Autumn	296	285	37.9	56.3	201.8	641.6	24.2	56.4	204.4	511.9	129.7	.038	.015

ward migration of herring along southwest Newfoundland during the winter, with a net movement westward. The monthly distribution of seiner catches over a period of years indicates a similar migration pattern. Some idea of the speed of the westerly migration can be obtained from the distance from the release area traveled by the tagged fish during its time at large (Table 3). Returns during the 1st wk revealed that some fish had moved as far west as Garia Bay, a distance of 65 naut. miles, which represents an average of 11 naut. miles/day, or approximately 0.5/h. Such a rapid migration rate undoubtedly accounts for the thorough mixing of the tagged herring with the untagged population and suggests that the net westward movement of herring along southwest Newfoundland is accomplished by actively migrating fish rather than fish passively transported by the prevailing westerly current which flows along the coast. Analyses of energy expenditures confirm these high levels of activity that result in a substantial depletion of fat reserves from an average (spring- and fall-spawners combined) of 14% in December to 8% in April (Parsons and Hodder 1975). This energy loss occurs in spite of the dormant state of the gonads (Parsons and Hodder 1975) during the overwintering period, implying very little diversion of somatic energy for gonad development. The reason for such high activity levels at this time of the year is uncertain but may be related to coincidental migrations of cod. In late fall there is a differential emigration of large cod (>80 cm) from the northern Gulf of St. Lawrence to the southwest coast of Newfoundland (R. Wells personal communication) where overwintering occurs. During this period these large cod feed very heavily (85–90%) on herring (Minet and Peradou 1977). Thus, the high degree of activity characterizing overwintering herring along southwest Newfoundland may be associated with avoidance behavior induced by the presence of abundant concentrations of predatory cod.

Acknowledgments

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Healing of Wounds and Location of Tags in Atlantic Herring (*Clupea harengus harengus*) Released with Abdominally Inserted Magnetic Tags

G. H. WINTERS

Department of Fisheries and the Environment, Fisheries and Marine Services, Research and Resource Services, Newfoundland Region, St. John's, Nfld. A1C 1A1

WINTERS, G. H. 1977. Healing of wounds and location of tags in Atlantic herring (*Clupea harengus harengus*) released with abdominally inserted magnetic tags. J. Fish. Res. Board Can. 34: 2402–2404.

Information derived from Atlantic herring (*Clupea harengus harengus*) released with abdominally inserted magnetic tags and recovered by an electronic tag-detection system indicated that sustained mortality due to internal damage caused by the tag or the incision wound was probably minimal. In addition, tags that have not become attached to the body wall and internal organs prior to spawning will to a large degree be extruded with the gonadal products during spawning.

Key words: tagging, wounding, mortality

WINTERS, G. H. 1977. Healing of wounds and location of tags in Atlantic herring (*Clupea harengus harengus*) released with abdominally inserted magnetic tags. J. Fish. Res. Board Can. 34: 2402–2404.

Les renseignements obtenus à la suite de marquages de harengs atlantiques (*Clupea harengus harengus*) avec marques magnétiques insérées dans l'abdomen et récupération à l'aide d'un système électronique de détection des marques indiquent que la mortalité résultant de dommages internes causés par la marque ou par l'incision est probablement minimale. En outre, les marques qui ne se sont pas fixées sur la paroi abdominale ou sur des organes internes avant la fraie seront pour la plupart expulsées en même temps que les produits sexuels au moment de la fraie.

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THE usefulness of mark–recapture experiments in fisheries is greatly dependent on the extent of tag retention and the extra mortality caused by the tagging operation, in relation to the condition of the tagged fish upon release (reflected in initial mortality) and to long-term effects due for example to wound infection (reflected in sustained mortality). Discrimination and quantification of these factors are essential in determining the design of tagging experiments and in analyzing subsequent recovery data.

During the early 1970s several tagging experiments involving abdominally inserted tags in Atlantic herring (*Clupea harengus harengus*) were conducted along southwest Newfoundland and the southern Gulf of St. Lawrence (Winters and Beckett 1977). As part of the experimental design an electronic tag-detection system capable of discriminating and selecting tagged fish from commercial landings of herring was installed in a reduction plant located at Isle aux Morts, Newfoundland. This communication documents the results of analyses of data on wound condition, tag location, and tag loss obtained from tagged fish recovered by the electronic tag-detection system.

Materials and methods — A description of the type of tags, method of application, and areas of release for the various tagging experiments considered here is given in Winters and Beckett (1977). Tagged fish retrieved by the electronic tag-detection system were examined in detail and the location of the tag within the body cavity was recorded. In addition, the condition of the incision wound in the body wall of tagged herring was classified into one of several categories according to the degree of healing.

Results and discussion — Tags recovered from fish that had been released for up to 2 mo and had not spawned since being tagged were mainly located loose in the body cavity, most of the rest being embedded in the gonad (Table 1). In fish that were at large for 6–7 mo and had not spawned, only one tag was observed loose in the body cavity, all the rest

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FIG. 1. Internal tag attached to body wall mesentery; the fish was tagged in August 1970 and recaptured in February 1971.

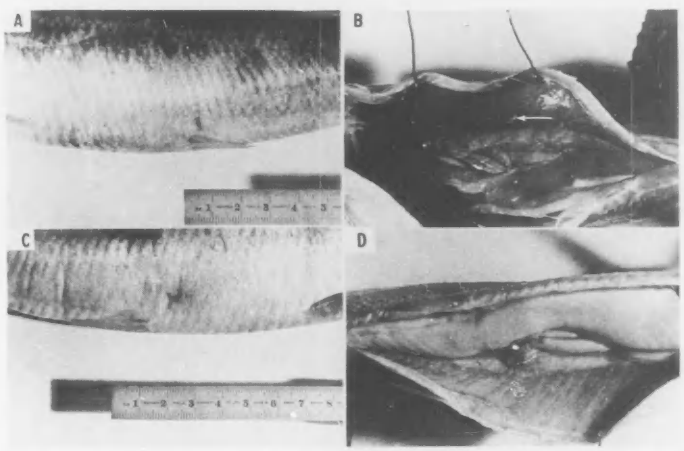

FIG. 2. Condition of the incision wound of tagged fish. A, External wound after 2 mo at large; B, internal incision after 2 mo at large; C, external scar after 6 mo at large; D, internal tag partially embedded in tagging incision after 6 mo at large.

being either embedded in the gonad or attached to the body wall (Fig. 1). In fish that were at large for 10–12 mo and had spawned since being tagged, all recovered tags were attached to either the body wall or the intestine. Evidently tags loose in the body cavity immediately after the tagging operation eventually become attached to the body wall and internal organs. However, only those tags attached to internal organs (including perhaps the gonads) and not loose in the body cavity nor embedded in the gonads will be retained through the spawning period. This observation is supported by analyses of data on tag recovery rates (Winters 1977) which indicated that most (96%) tags inserted in ripening herring were extruded with the reproductive products, whereas those applied to recently spent or recovering herring had higher retention rates. Consequently, long-term returns from tagging experiments using magnetic tags inserted abdominally will be restricted to the proportion of the inserted tags that become attached to internal structures prior to spawning. Tagging fish shortly after they had completed spawning would ensure maximum tag returns.

Analyses of the condition of the incision wound indicated that none of the tagged herring released during the Bay de Loup experiment showed any

TABLE 1. Location of tag in recaptured herring in relation to months at large.

Area of release	Date of release	Mo at large	Spawned since tagging?	Location of tag: Attached to body wall or intestine	Attached to or embedded in gonad	Loose in body cavity	Partially emdedded in wound	Total
Bay de Loup	Jan. 1971	1	No		3	31	1	35
Bay de Loup	Jan. 1971	2	No		1	10	1	12
Gaspé	Aug. 1970	6	No	1	3			4
Gaspé	Aug. 1970	7	No	5	10	1		16
Magdalens	May 1970	10	Yes	1				1
Rôti, La Poile bays	Mar. 1970	11	Yes	2				2
Rôti, La Poile bays	Mar. 1970	12	Yes	3				3
	Total			12	18	42	2	73

signs of infection up to 2 mo after tagging, although the wound was open externally (Fig. 2A) and internally (Fig. 2B), and showed no signs of healing:

Mo. at large	Condition of wound: Open, not infected	Healed scar: Visible	Healed scar: Invisible	Internal damage
1	35			2
2	12			
6		3	1	
7		3	13	
10			1	
11			2	
12			3	

The only internal damage noted was a small cut in the testes of two fish. This cut was not considered to be serious enough to affect survival. Most of the tagged fish from the Gaspé releases recaptured along southwest Newfoundland 6–7 mo later were completely healed and no scarring was evident. In the remainder of the tagged fish the wound was closed and apparently healed, although the scar was clearly evident (Fig. 2C). In one instance in which no external wound was visible, internal examination revealed that the tag was still partly embedded in the incision (Fig. 2D) and tissue growth had healed the wound and attached the tag to the body wall. There was no evidence, either externally or internally, of any incision scar in fish that had been at large at least 10 mo, and internal aftereffects of tagging were not observed.

The rapid healing and the lack of infection and damage to the internal organs suggest that the abdominal incision made during tagging does not cause significant mortality and that such mortality as may occur would be soon after tagging rather than later.

Acknowledgments — I am grateful for the assistance of the technical staff of the Pelagic Section, Newfoundland Biological Station, in the collection and collation of the data contained in this document.

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Effects of Phosphorus from Apatite on Development of Freshwater Communities

E. A. SMITH, C. I. MAYFIELD

Department of Biology, University of Waterloo, Waterloo, Ont. N2L 3G1

AND P. T. S. WONG

Department of Fisheries and the Environment, Fisheries and Marine Service, Canada Centre for Inland Waters, Great Lakes Biolimnology Laboratory, Burlington, Ont. L7R 4A6

SMITH, E. A., C. I. MAYFIELD, AND P. T. S. WONG. 1977. Effects of phosphorus from apatite on development of freshwater communities. J. Fish. Res. Board Can. 34: 2405–2409.

Phosphorus-free nutrients were added to three epilimnetic (pH 7.8) 40-ℓ tanks. Apatite crystals (30–100 μm) were added at loading rates of 30, 2, and 0 mg·day^{-1}. After a 60-day incubation at 20°C, levels of particulate organic carbon, particulate nitrogen, and particulate organic phosphorus in Tank 1 increased from 0.42, 0.090, and 0.015 to 6.10, 0.820, and 0.430 μg·ml^{-1}, respectively. This increase was due to the proliferation of algae, bacteria, and zooplankton and did not occur in the tank with only P-free nutrients. Algae and bacteria grew extensively on the surfaces of apatite crystals causing crystals to aggregate. Zooplankton increases followed those in algae and bacteria, and grazing was restricted to the areas around the apatite crystals. Results suggest that the contribution of soluble ortho-PO_4^{3-} from apatite to the P-cycle of aquatic environments would be more important under oligotrophic conditions than in areas receiving high loadings of anthropogenic-PO_4^{3-}, particularly where high erosion increases apatite loadings.

Key words: apatite, calcium phosphate, hydroxyapatite, fluorapatite, algae, biogeochemistry, freshwater communities

SMITH, E. A., C. I. MAYFIELD, AND P. T. S. WONG. 1977. Effects of phosphorus from apatite on development of freshwater communities. J. Fish. Res. Board Can. 34: 2405–2409.

Nous avons introduit dans trois bassins épilimnétiques (pH 7.8) de 40 ℓ des éléments nutritifs dépourvus de P. Des cristaux d'apatite (30–100 μm) ont été ajoutés à des taux de charge de 30, 2, et 0 mg·jour^{-1}. Après incubation de 60 jours à 20°C, les teneurs en carbone organique particulaire, nitrogène particulaire et phosphore organique particulaire dans le bassin 1 passent de 0.42, 0.90 et 0.015 à 6.10, 0.820 et 0.430 μg·ml^{-1} respectivement. Cette augmentation est due à la prolifération des algues, des bactéries et du zooplancton, et ne se produit pas dans le bassin contenant seulement des éléments nutritifs dépourvus de P. Les algues et les bactéries croissent abondamment sur la surface des cristaux d'apatite, causant ainsi une agrégation des cristaux. L'augmentation du zooplancton suit celle des algues et des bactéries, et le broutage se limite aux régions autour des cristaux d'apatite. Les résultats donnent à croire que la contribution de l'ortho-PO_4^{3-} soluble, provenant de l'apatite, au cycle du P des milieux aquatiques serait plus grande dans des conditions oligotrophes que dans des régions recevant de fortes charges de PO_4^{3-} anthropique, particulièrement dans les endroits où une forte érosion augmente les charges d'apatite.

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APATITES (eg. hydroxyapatite ($Ca_{10}(PO_4)_6(OH)_2$) and fluorapatite ($Ca_{10}(PO_4)_6F_2$)) have been under active investigation for many years because of their importance in the understanding of the crystal chemistry of tooth and bone material (Beevers and McIntyre 1964; McConnell 1970; Robertson et al. 1972; Tomažič and Nancollas 1975), but the role of naturally occurring apatite in the P-cycle of aquatic ecosystems has not been completely established.

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Although the mineral is widely distributed in nature (see McConnell [1973] for review of apatite literature) and enters water systems in groundwater, runoff, and erosion material (Altschuler 1973), it has been suggested that apatite would not contribute a significant amount of ortho-PO_4^{3-} to freshwater environments due mainly to its relatively low solubility in alkaline solutions (Williams et al. 1976b). Other workers have suggested that increases in total plankton in the western basin of Lake Erie can be attributed in part to increasing degrees of saturation of the water with respect to hydroxyapatite (Snow

and Thompson 1968). Although anthropogenic-PO_4^{3-} is much more significant in primary production than less-available forms such as apatite-PO_4^{3-}, reduction in nonapatite phosphorus loading rates as proposed by the Great Lakes Water Quality Agreement (U.S. Dep. of State 1972) would increase the relative contribution of natural phosphorus sources such as apatite, especially in high erosion areas.

The present investigation was conducted to determine the effects of two loading rates of a naturally occurring apatite on the development of freshwater communities receiving additional loadings of P-free nutrients.

Materials and methods — Apatite obtained from the Royal Ontario Museum as representative of apatite found in the Lake Ontario area was ground and sieved to obtain crystals of 30–100 μm. The sample was analyzed for Ca, P (as ortho-PO_4^{3-}), Na, Cd, Mg, K, Al, Fe, Hg, Si, Cu, Zn, Ni, and Pb by X-ray diffraction (Anon. 1974).

Three 40-ℓ glass tanks were filled with epilimnetic water from the north shore of Lake Ontario. The water had a pH of 7.8 and contained 42 and 0.008 $\mu g \cdot ml^{-1}$ of soluble Ca^{2+} and dissolved ortho-PO_4^{3-}, respectively (Table 1). Incubation was at 20°C with 18 h light (3800 lx) and 6 h darkness. Each tank received the following P-free nutrients at 24-h intervals during a 14-day incubation (nutrients are based upon the composition of Bristol's medium (Nichols and Bold 1965) and all values are expressed as total micrograms added per day per tank): $NaNO_3$, 10; $CaCl_2 \cdot 2H_2O$, 5; NaCl, 1; $MgSO_4 \cdot 7H_2O$, 3; EDTA, 2; $FeSO_4 \cdot 7H_2O$, 0.2; H_3BO_3, 4; $ZnSO_4 \cdot 7H_2O$, 0.15; $CuSO_4 \cdot 5H_2O$, 0.25; $MnCl_2 \cdot 4H_2O$, 0.10; NH_4MoO_4, 0.10; $Ca(NO_3)_2 \cdot 6H_2O$, 0.05. The level of contaminating phosphorus in the stock nutrient solution (pH 7.8) was <0.001 $\mu g \cdot ml^{-1}$ total P. After 14 days the P-free nutrient loadings were increased 100-fold for an additional 46 days.

In addition to the P-free nutrients, Tanks 1 and 2 received 30 and 2 mg of apatite crystals $\cdot day^{-1}$, respectively. Tank 3 received no apatite loadings and served as the control. Water samples from each tank were periodically analyzed for soluble ortho-PO_4^{3-}, dissolved Ca^{2+}, particulate organic carbon (POC), particulate nitrogen (PN), particulate organic phosphorus (POP), and chlorophyll *a* (Anon. 1974). Zooplankton numbers were estimated microscopically from three 25-ml water samples collected from each of the tanks; ^{14}C-acetate mineralization was used as an index of heterotrophic activity according to the method of Harrison et al. (1971). Tank walls were scraped every 48-h to minimize periphyton growth, and water lost by evaporation was replaced with distilled water, pH 7.8.

A 2.5-ml water sample from each tank was collected on Millipore filters (0.45 μm). After washing, fixing, dehydration, and drying, the specimens were mounted, coated, and examined with an AMR 1000 scanning electron microscope (Smith et al. 1977).

Results — Chemical analyses showed that Ca^{2+} (428 $mg \cdot g^{-1}$) and ortho-PO_4^{3-} (196 $mg \cdot g^{-1}$ as ortho-PO_4^{3-}) were the major ionic constituents of the apatite. Other constituents detected in milligrams per gram were Al (0.88), Fe (0.64), Mg (0.40), Cu (0.004), Pb (0.08), Zn (0.012), Ni (0.028), Si (6.8), Hg (0.0006), Na (4.8), K (1.2), and Cd (0.012).

TABLE 1. Some characteristics of Lake Ontario water sample.

Parameter	Concn ($\mu g \cdot ml^{-1}$)
Soluble Ca^{2+}	42.0
Soluble ortho-PO_4^{3-}	0.008
Total P	0.023
POC[a]	0.420
PN[a]	0.090
POP[b]	0.015
pH	7.8
Chlorophyll *a*	3.1 $\mu g \cdot \ell^{-1}$
Zooplankton	12.0 organisms $\cdot \ell^{-1}$
^{14}C-acetate mineralization	2.5 $\mu g \cdot \ell^{-1} \cdot h^{-1}$

[a]GF/C filtered.
[b]POP = total P − soluble ortho-PO_4^{3-}.

Numbers of algae, bacteria, and zooplankton were positively related to apatite loading (Fig. 1). Although Tank 3 (control) received the same loading rate of P-free nutrients as other tanks, PO_4^{3-}-limitation restricted development. Levels of POC, PN, and POP did not increase significantly during the first 14 days in the control tank and a 100-fold increase in the P-free nutrient loading also failed to cause substantial increases in these parameters. In the control the tank levels of chlorophyll remained <10 $\mu g \cdot \ell^{-1}$ but ^{14}C-acetate mineralization increased from 2.5 to 7.6 $\mu g \cdot \ell^{-1} \cdot h^{-1}$, indicating that the heterotrophic population was using autochthonous carbonaceous material for growth. In Tank 2, POC, PN, and POP increased substantially following the increase in loading of P-free nutrients, so that after 60 days they were 3.5, 0.36, and 0.100 $\mu g\ ml^{-1}$, respectively. These increases corresponded to increases in chlorophyll *a* as well as ^{14}C-acetate mineralization and zooplankton. These findings were attributable entirely to the addition of ortho-PO_4^{3-} from the partial dissolution of apatite crystals.

The 15-fold higher loading rate of apatite in Tank 1 resulted in the development of a complex aquatic community composed of several species of algae, bacteria, and zooplankton. After 60 days, POC, PN, and POP had increased from 0.8, 0.17, and 0.015 $\mu g \cdot ml^{-1}$ to 6.1, 0.82, and 0.430 $\mu g \cdot ml^{-1}$, respectively. Similarly, the levels of chlorophyll *a* increased from 3.1 to 98 $\mu g \cdot \ell^{-1}$, ^{14}C-acetate mineralization from 4 to 18 $\mu g \cdot \ell^{-1} \cdot h^{-1}$, and zooplankton from 15 to 82 $\cdot \ell^{-1}$.

Microscopic examination of water samples revealed that algae and bacteria rapidly colonized apatite crystals in Tank 2 and the extensive growth of algae and bacteria on apatite crystals caused the crystals to become aggregated. After 42 days small aggregates coalesced due to the proliferation of

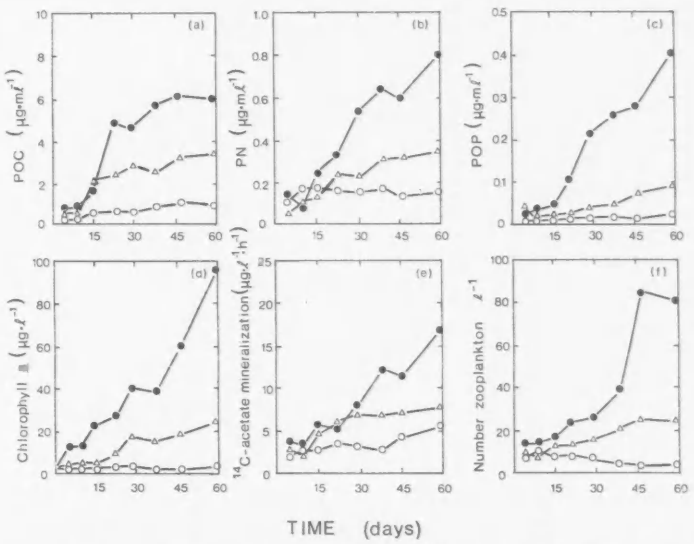


FIG. 1. Responses of the tank communities to different apatite loadings. Tank 1 (30 mg apatite·day^{-1}) ●——●; Tank 2 (2 mg apatite·day^{-1}) Δ——Δ; Tank 3 (no apatite — control) ○——○).

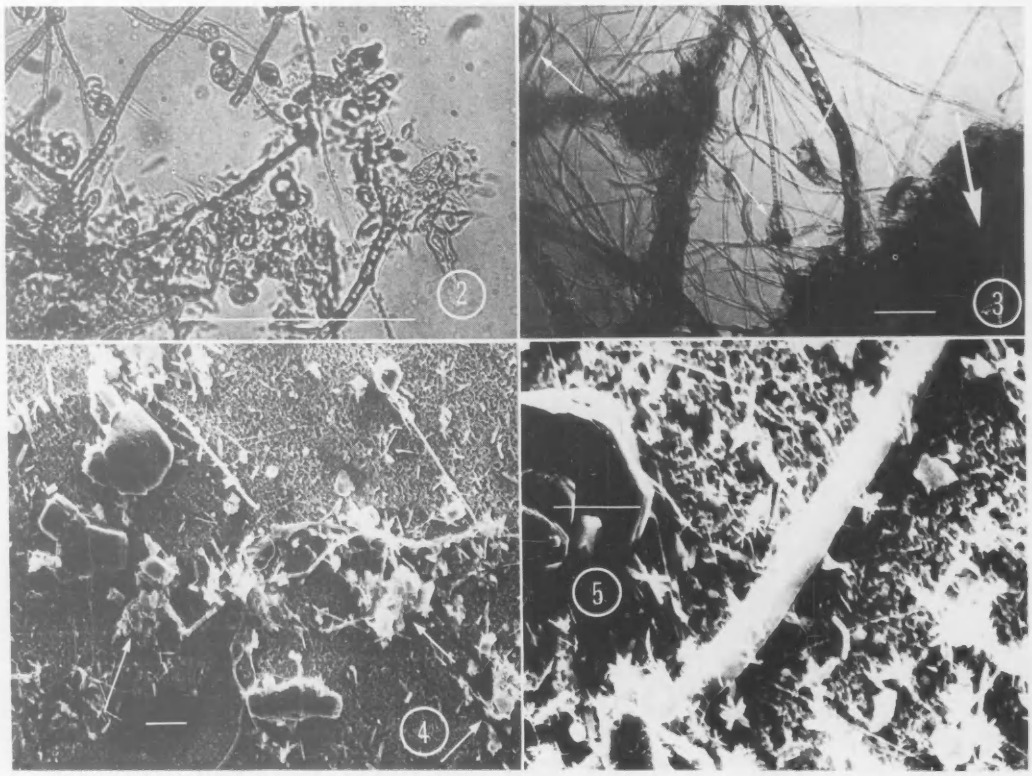
filamentous algae in particular (Fig. 2). Similar conditions existed in Tank 1 but not in Tank 3, which received no apatite loadings.

The growth of algae and bacteria on the crystal surfaces restricted distribution of zooplankton almost exclusively to areas around the crystals in Tank 2. Motile zooplankton were also found to manipulate crystals to eat algae growing on the crystal surfaces. After 50 days, growth of filamentous and unicellular algae was extensive, allowing attachment of sedentary zooplankton (Fig. 3).

Scanning electron microscopic examination of samples from Tanks 1 and 2 after 5 days revealed details of microbial colonization of apatite crystals and development of crystal aggregation (Fig. 4). After 14 days in Tank 2 small apatite crystals had become aggregated into clusters which appeared to be attached to organic material and after 23 days, extensive microbial growth on crystal surfaces caused further aggregation. Similarly, after 14 days in Tank 1, clusters of apatite crystals had become attached to various surfaces, including cell walls of filamentous algae (Fig. 5).

Discussion — Although apatite characteristically displays low solubility in aqueous solutions particularly under alkaline conditions (Brown 1966), sufficient ortho-PO_4^{3-} was released by the partial dissolution of apatite crystals in lake water of pH 7.8 to cause considerable increases in the numbers of algae and bacteria. Several factors will affect the solubility of apatite crystals in aqueous environments, such as pH, particle sizes, quantities, ions in solution, temperature, crystal impurities, and degree of saturation of the water with respect to apatite (Brown 1966; Rootare et al. 1962; Wier et al. 1971; Hagen 1975). There is little information available describing whether or not various lakes are saturated with respect to apatite, but some workers have determined that Lake Ontario (Sutherland et al. 1966) and the eastern and central basins of Lake Erie are undersaturated with respect to hydroxyapatite (Snow and Thompson 1968). Comparisons of apatite saturations and plankton concentrations in Lake Erie have suggested that increases in total plankton correspond to increases in the degree of saturation of the water with respect to hydroxyapatite (Snow and Thompson 1968). If the level of soluble ortho-PO_4^{3-} drops below the value determined by the solubility product of a mineral phase such as apatite, equilibrium is no longer maintained and mineral dissolution occurs. This implies that apatite has the potential for contributing to the P-cycle of aquatic environments that are undersaturated with respect to apatite.

The ortho-PO_4^{3-} released from partial dissolution of crystals in epilimnetic water from Lake Ontario (undersaturated with respect to apatite) caused substantial increases in the biomass in those tanks that received continuous apatite loadings. Chlorophyll *a* determinations showed that algae in the tanks receiving apatite increased before the hetero-



FIGURES 2–5

FIG. 2. Unicellular and filamentous algae in Tank 2 after 42 days. Scale = 40 μm. FIG. 3. Growth of algae on apatite crystals (large arrow) and grazing zooplankton (small arrows) after 50 days in Tank 1. Scale = 40 μm. FIG. 4. Scanning electron micrograph of crystal aggregates (arrows) after 5 days in Tank 1. Scale = 10 μm. FIG. 5. Clusters of small apatite crystals attached to the surface of algal filaments in Tank 1 after 14 days. Scale = 10 μm.

trophic population (Fig. 1, d, e). Bacterial growth following algal development is usually due to the use of algal secretory products (Maksimova and Pimenova 1969; Nalewajko and Lean 1972) as well as organic detritus (Mills and Alexander 1974). Large increases in zooplankton did not occur until after the algae and bacteria were well established.

The close association of algae, bacteria, and zooplankton with apatite crystals may be important in affecting their distribution, since it has been shown that the major portion of the apatite that enters Lake Erie as erosion material from the central bluffs is transported to the eastern basin by currents (Williams et al. 1976a).

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A Simple Device for Retrieving Instruments or Traps Set Under Ice

M. BUSDOSH

Department of Biology and Water Resources Laboratory, University of Louisville, Louisville, Ky. 40208, USA

AND A. E. MANNING

Naval Arctic Research Laboratory, Barrow, Alaska 99723, USA

BUSDOSH, M., AND A. E. MANNING. 1977. A simple device for retrieving instruments or traps set under ice. J. Fish. Res. Board Can. 34: 2409–2410.

Recovery of instruments or traps suspended under ice is often difficult because refreezing at the circumference of the hole decreases the hole diameter to less than trap diameter, and freezes around the attached line. Line freezing can be reduced by suspending the instrument from the center of the hole. A device consisting of two lengths of wood hinged together, with recurved nails at the lower end can then be used to catch and recover the instrument line through an adjacent hole. These procedures reduce retrieval time by two thirds, and eliminate the damage to instruments or trapped animals that often occurs during recovery. The device can be easily made or repaired on site.

Key words: under-ice sampling, under-ice trapping, instrument recovery, arctic

BUSDOSH, M., AND A. E. MANNING. 1977. A simple device for retrieving instruments or traps set under ice. J. Fish. Res. Board Can. 34: 2409–2410.

Il est souvent difficile de récupérer des instruments ou des pièges sous la glace: la recongélation à la périphérie du trou en diminue le diamètre à moins du diamètre du piège, et il

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se forme de la glace autour de l'orin. On peut réduire la formation de glace autour de l'orin en suspendant l'instrument au centre du trou. Un appareil constitué de deux pièces de bois jointes par une charnière et muni de clou recourbés à l'extrémité inférieure peut être utilisé pour récupérer l'orin à travers un trou adjacent. Cette méthode réduit des deux tiers le temps de récupération et protège les instruments ou les animaux piégés contre les dommages qui se proudisent souvent au moment de la récupération. On peut facilement construire ou réparer l'appareil sur le site.

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RETRIEVAL of subsurface instruments or traps through ice is often difficult. An auger powered by a two stroke posthole digger engine can drill a hole of 200–225 mm diam through 2 m of ice within 15 min to set instruments, but unless a set is retrieved within several hours, new ice forms, freezing around the line and reducing the hole diameter so that the instrument cannot be pulled up.

The usual method for recovery has been to chip away the new ice with an ice chisel, thus enlarging the hole and freeing the line. With 2 m of ice and a set time of 48 h this often takes more than an hour of hard work, and often results in loss of the attached instrument by accidently severing the line. Ganton (1968) has reviewed other methods of keeping holes through ice open, each with varying success and expense. We describe a way to simplify recovery by the use of a simple device through an adjacent hole.

The device (Fig. 1) consists of two pieces of wood, a hinge, and four nails. The length of the vertical piece is determined by ice thickness; the horizontal piece should be about 1 m in length. Two nails are placed on the horizontal piece on each side adjacent to the side on which the hinge is set. The heads of the nails are slightly bent back toward the hinge.

The device is used through a hole drilled approximately $\frac{1}{2}$ m from the original. With the hinge straightened it is pushed down the hole until the hinge is just below the bottom of the ice. The buoyancy of the wood will cause the hinge to flex, allowing the lower piece to lie against the ice. The device is then rotated through 90°, causing the wood to contact the line (Fig. 1). When this contact is felt, the device is pulled up, and one of the nails catches the line as it is pulled by. As long as the rotation is kept under 360°, the line will slide over the nail, allowing it to be brought to the surface.

Besides the saving in time and work, this method allows the instrument to be brought up on the first attempt. With the method of gradually enlarging the original hole, recovery is rarely successful on any of the first several attempts, causing the set to be banged on the underside of the ice — damaging to an instrument and often injurious to animals in a trap. Also, if it is desired to reset in this same location, a "clean" hole is available.

The problem of line freezing can be greatly reduced for the first several hours, depending on ice growth rates, by suspending the instrument from the center of the hole rather than along a side. This can be accomplished by suspending the line from a board placed across the hole, rather than from a stake beside the hole.

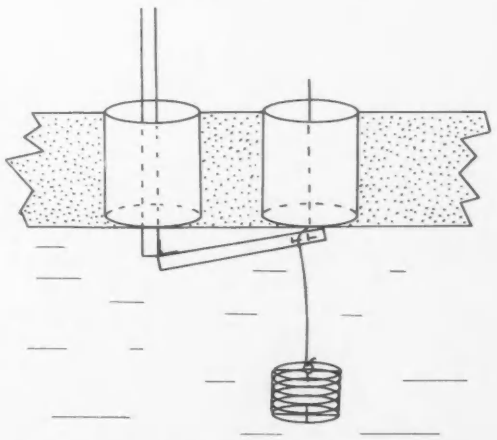

FIG. 1. Catching of instrument line by retrieval device through an adjacent hole.

Unless the instrument or trap is set at a depth below the ice at least twice as great as the ice thickness, it is helpful to have an excess of a few meters of line at the top.

Using these methods, the time necessary to retrieve an instrument can be decreased by two thirds or more. The only chipping required is to free the line from the few centimeters of new ice formed at the top of the hole. The adjacent hole is then drilled, and the instrument recovered.

The keys to this device are its efficiency and simplicity. The experience of a complicated device malfunctioning is familiar to anyone who has done field work under harsh conditions. This device has little to malfunction and can be easily made or repaired in minutes.

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Evidence for the Assumption of Independence between Gastric Emptying Rate and Swimming Activity Using Atlantic Cod, *Gadus morhua*

A. V. TYLER[1]

Department of Fisheries and the Environment, Fisheries and Marine Service, Biological Station, St. Andrews, N.B. E0G 2X0

TYLER, A. V. 1977. Evidence for the assumption of independence between gastric emptying rate and swimming activity using Atlantic cod, *Gadus morhua*. J. Fish. Res. Board Can. 34: 2411–2413.

Juvenile Atlantic cod, *Gadus morhua*, were forced to swim at speeds of 0.07, 0.6, and 1.2 body lengths/s after eating measured quantities of food. Higher speeds could not be maintained for more than 2 days. Only the highest speed caused a decrease in gastric emptying rate, but the decrease was not of sufficient magnitude to interfere with ration estimates based on digestion rate data.

Key words: feeding, swimming speed, digestion rate

TYLER, A. V. 1977. Evidence for the assumption of independence between gastric emptying rate and swimming activity using Atlantic cod, *Gadus morhua*. J. Fish. Res. Board Can. 34: 2411–2413.

On a forcé des jeunes morues franches, *Gadus morhua*, à nager à des vitesses de 0.07, 0.6 et 1.2 longueurs de corps/s après qu'elles aient absorbé des quantités mesurées de nourriture. Les poissons n'ont pu maintenir les grandes vitesses pendant plus de 2 jours. Seule la plus grande vitesse entraîne une diminution de la vitesse du transit intestinal. La diminution n'est toutefois pas suffisante pour fausser les estimés de ration fondés sur les vitesses de digestion.

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A number of workers have made the assumption that gastric emptying rates, or daily ration estimates based on these rates, are independent of swimming activity (Bajkov 1935; Healey 1971; Swenson and Smith 1973; Tyler 1970; and others). The purpose of this study was to test this hypothesis in order to tighten the basis for interpreting gastric emptying data for feeding rate estimates.

Treatment of fish — Underyearling Atlantic cod, *Gadus morhua*, from Passamaquoddy Bay, N.B., were captured, fed, and acclimated as previously described (Tyler 1970).

Before an experiment, one fish was placed into each exercise trough where it was acclimated to 10°C at a rate of 1 C deg/day at a constant water velocity of 10 cm/s. Young cod are commonly found at this temperature during summer feeding and growth. Water velocity was measured with an Ott propeller type current meter. Fish were fed cut pieces of shrimp (*Pandalus*) abdomen stored frozen a few hours after capture. An experiment was not begun until the fish fed well voluntarily.

For an experiment, fish were given 3–20, 1-cm cubes of shrimp. Percentage of water was determined so that dry weights of the meal could be calculated. The fish were killed 6 h after being fed and stomach contents were dried to constant weight.

Apparatus — An axial-flow pump directed water to a header tank. Water flowed from the header over a spillway into nine, parallel, plexiglass (lucite) troughs. Water passed out of the troughs via standpipes and into a collecting sump, from which it was drawn into the pump through an underwater port at the bottom of the sump. The water flow was controlled by adjusting the water level in the sump, in effect altering the height of the head that the pump worked against. The pump ran at constant rpm. Depth in the sump was maintained by a standpipe. The standpipe height was altered by stacking nesting links of polyvinyl chloride pipe on top of the sump standpipe. The smaller the distance between the sump level and the header level, the greater the flow in the trough. Flow turbulence was reduced by horizontal and vertical plexiglass baffles in the forward position of the trough. A potassium permanganate solution introduced at the downstream edge of the baffles during trial runs spread to one third of the trough at the downstream retaining screen. All metal and wood surfaces were painted with white epoxy resin.

The compartment of the trough that the fish were placed in measured 12 × 18 × 100 cm. New seawater was added to the trough apparatus at the rate of 10 ℓ/min and was controlled to ±0.5°C.

The entire apparatus was in a closed room. During an experiment low level, incandescent lights (25 W), 1.5 m above the apparatus, were on constantly. Troughs and fish were monitored by closed-circuit TV. The occasional indi-

[1]Present address: Department of Fisheries and Wildlife, Marine Science Center, Oregon State University, Newport, Oreg. 97365, USA

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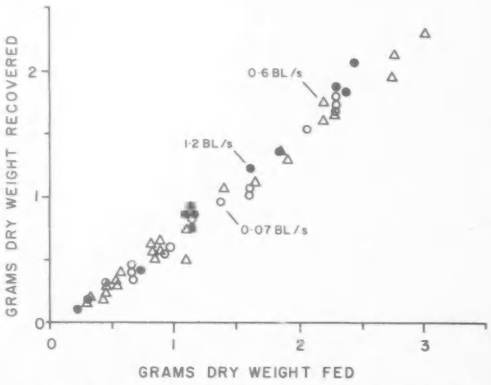

FIG. 1. Dry weight of food recovered from stomachs 6 h after meal was given as a function of the dry weight of food fed, for fish exercised at one of three swimming speeds.

vidual that rested on the back screen or on the bottom of the trough was not processed further in the experiment.

Approximation of swimming speed range — To estimate the range of swimming speeds that the fish could sustain, four cod, 24–32 cm long, were placed one at a time in a tunnel-type exercise apparatus designed after Farmer and Beamish (1969). The apparatus is essentially a closed, tubular loop containing a pump and a large, tubular exercise chamber. The fish were held overnight in the exercise chamber with just enough water current to cause them to swim. The following morning the current was increased.

The first fish swam at 1.24 body lengths (BL)/s (33 cm/s) for 24 h and then 1.5 BL/s for 4 h, after which the fish fell back against the retaining screen. The second fish swam at 1.5 BL/s (36 cm/s) for 48 h before it collapsed against the screen. The third fish swam at 0.62 BL/s (16 cm/s) for 24 h and 1.5 BL/s (36 cm/s) for 26 h, when it collapsed. The fourth fish was exercised for 12 h at 0.5 BL/s (16 cm/s) and then at 1.5 BL/s for 45 min, when it collapsed.

Since 1.5 BL/s was apparently more than the fish could sustain on a long-term basis (48 h), the gastric emptying experiments were planned at speeds lower than this. The top swimming speed for the gastric emptying experiments was set at 1.2 BL/s.

Experimental design — Three series of experiments were planned with the nine-channel exercise apparatus. In series 1 the fish were given just enough current (2 cm/s, mean 0.07 BL/s) to cause them to orient themselves in the trough. They sometimes moved with the current, but most of the time faced into it. In series 2 they were given a current of 20 cm/s, equivalent to a mean of 0.6 BL/s. In series 3 they were given 30 cm/s, equivalent to a mean of 1.2 BL/s. The 14 cod used in the first series were 27–30 cm long. The 25 cod in the second series were 29–33 cm long. The 12 cod in the third series were 23–26 cm long. Because of variation in body length, variation in relative swimming speed was as follows: series 1, ±0.004 BL/s; series 2, ±0.037 BL/s; series 3, ±0.075 BL/s.

Data analysis was carried out on the assumption that gastric emptying follows a negative exponential depletion curve, i.e. that percentage disappearance is constant in time. (Beamish 1972; Brett and Higgs 1970; Elliot 1972; Tyler 1970; Windell et al. 1976). In that case,

$$N_{T+1} = N_T e^{-b \cdot t} \quad (1)$$

expresses the relationship between food recovered from the stomach (N_{T+1}), food fed (N_T), time interval between feeding and sampling (t), and instantaneous depletion rate (b). The quantity, $e^{-b \cdot t}$ is the proportionate remainder rate (or the percentage rate if multiplied by 100). Then $1 - e^{-b \cdot t}$ is the proportionate depletion rate. A graph of food recovered at a constant interval, t, vs. meal size will have a slope equal to the proportionate remainder rate, and an intercept of zero.

Results and conclusion — Since the slope of the regression between food fed and food recovered is the proportionate rate, the slopes of the three regressions were tested for equality (F-test, Dixon and Massey 1957, p. 218). No significant differences were found ($F = 2.27$, $F\,95(2,46) = 3.19$), but there was a significant difference at the 5% level in the mean weights of food recovered when adjusted by the within-groups regression coefficients ($F = 6.25$*). A comparison of regressions shows that the main difference occurs at the 1.2 BL/s level of exercise. Regression equations for 0.07 BL/s, 0.6 BL/s, 1.2 BL/s are $Y = -0.13 + 0.80\,X$, $Y = -0.14 + 0.87\,X$, and $Y = -0.17 + 0.83\,X$, respectively. There is slightly more food left in the stomachs when fish are heavily exercised (Fig. 1).

Daily ration estimates can be made by multiplying $(1 - e^{-b \cdot t}) \cdot N_T$ for a sequence of time intervals (say, each hour) throughout a 24-h period. N_T can be estimated from (hourly) stomach content samples.

Since the effect of swimming speed on gastric emptying is slight, these ration estimates can apparently be made without reference to the cod's recent activity levels.

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Recent Invasion of a Red Alga (*Bangia atropurpurea*) in Lake Michigan[1]

C. KWEI LIN

Great Lakes Research Division, University of Michigan, Ann Arbor, Mich. 48109, USA

JOHN L. BLUM

Department of Botany, University of Wisconsin, Milwaukee, Wis. 53201, USA

LIN, C. K., AND J. L. BLUM. 1977. Recent invasion of a red alga (*Bangia atropurpurea*) in Lake Michigan. J. Fish. Res. Board Can. 34: 2413–2416.

Bangia atropurpurea was first found on the southwestern shore of Lake Michigan in 1968; by 1976 it had covered suitable substrates on the southern two thirds of the lakeshore. Optimal vegetative growth occurred above the low waterline during the spring and fall, especially near harbor areas. Vegetative growth is initiated from either perennating basal cells or monospores. *Bangia* contained extraordinarily high concentrations of bromine and zinc, suggesting it requires relatively high levels of halogens and trace metals, which are present in runoff waters and contaminated harbors.

Key words: *Bangia*, invasion, Lake Michigan, halogens, trace metals, algal zonation

LIN, C. K., AND J. L. BLUM. 1977. Recent invasion of a red alga (*Bangia atropurpurea*) in Lake Michigan. J. Fish. Res. Board Can. 34: 2413–2416.

On a trouvé *Bangia atropurpurea* pour la première fois sur la rive sud-ouest du lac Michigan en 1968. En 1976, l'algue avait recouvert les substrats convenables sur les deux tiers méridionaux de la rive du lac. La croissance végétative optimale a lieu sous la ligne de basse eau au printemps et en automne, surtout dans le voisinage des ports. La croissance végétative se fait à partir de cellules basales vivaces ou de monospores. *Bangia* a une teneur extrêmement élevée en brome et en zinc, ce qui donne à croire que l'algue requiert des niveaux relativement élevés d'halogènes et de traces de métaux, présents dans les eaux de ruissellement et dans les ports contaminés.

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AN attached filamentous red alga, *Bangia atropurpurea* (Roth) Ag. (DeToni 1897), has recently invaded and become rapidly established as a dominant member of the algal flora at the waterline in harbor areas of the lower Great Lakes. Although *B. atropurpurea* has been recorded in many isolated instances in European streams and lakes (Pascher and Schiller 1925; Koster 1952; Belcher 1960; Kann 1959; Geesink 1973), its present occurrence in the North American Great Lakes is probably the most extensive growth in the freshwater environment. This communication reports our observations of the latest distribution and growth pattern of this alga in Lake Michigan.

History in the Great Lakes — Growth of *Bangia* occurred in Lake Erie during the 1960s. It was observed in Buffalo Harbor in 1964 (J. L. Blum unpublished data) and

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spread to the western basin in the late 1960s (Kishler and Taft 1970; Verduin 1975). It occurred in southwestern Lake Huron in 1975 (C. K. Lin unpublished data), on the southern shore of Lake Ontario in 1968 (K. E. Damann, SUNY-Brockport, N. Y. personal communication), and in Toronto Harbour in 1977 (C. K. Lin unpublished data). In Lake Michigan the first record of *Bangia* was made in 1968 on the Chicago waterfront by M. Long (Illinois Environmental Protection Agency); only a few filaments were noticed along the Milwaukee north breakwater in 1971. But by 1974 it had grown to be so dense that its reddish colour caused a modification in appearance of the Milwaukee waterline.

Results and discussion — Distribution — Our systematic investigation of *Bangia* distribution (Fig. 1) indicates that the plant is now present in harbors along the entire Wisconsin shore as far north as Baileys Harbor (45°04′ N) and along the Michigan shore as far north as Frankfort (44°37′ N).

Growth — *Bangia* colonizes a wide variety of substrates, including rubble, concrete, stonework, and algal filaments such as *Cladophora glomerata* (L.) Kütz., with the most conspicuous growth in the splash zone of breakwaters in the immediate vicinity of port cities. The breakwaters, constructed of concrete, rubble, or stone, and sometimes protected by an outer shell of interlocking steel plates, extend out into the lake and may serve as a channel for harbor traffic as well as the discharge of a tributary stream. *Bangia* grows much better on a rough surface of broken rocks or eroded concrete than on any smooth surface observed. Attachment to solid substrates is secured by rhizoidal outgrowths protruding from the basal cells of filaments. *Bangia* as well as other filamentous algae are largely excluded from sandy portions of the Lake Michigan littoral, presumably because of the unstable substrate.

Though *Bangia* appears to grow best in the spring and fall, populations remain in position during much of the ice-free seasons and are visible in a zone 5–10 cm wide at and above the prevailing water level. When *Cladophora* is present in the warmer months, the light auburn or rusty-purple band of *Bangia* is in sharp contrast with the green *Cladophora* zone below (Fig. 2a). When water levels remain low during periods of calm weather, desiccation of waterline algae may occur. *Bangia atropurpurea*, like the marine entity *B. fuscopurpurea*, exhibits remarkable ability to withstand such desiccation (Biebl 1962).

Perennation of *Bangia* is accomplished by basal vegetative parts which penetrate into or become encrusted by the substrate. In early spring these parts give rise to erect thalli of uniseriate filaments ca. 10 μm in diameter which later develop to multiseriate thalli up to ca. 120 μm thick, 10 cm tall. Formation and release of monospores commonly occurs from mature thalli (Fig. 2b) and these spores

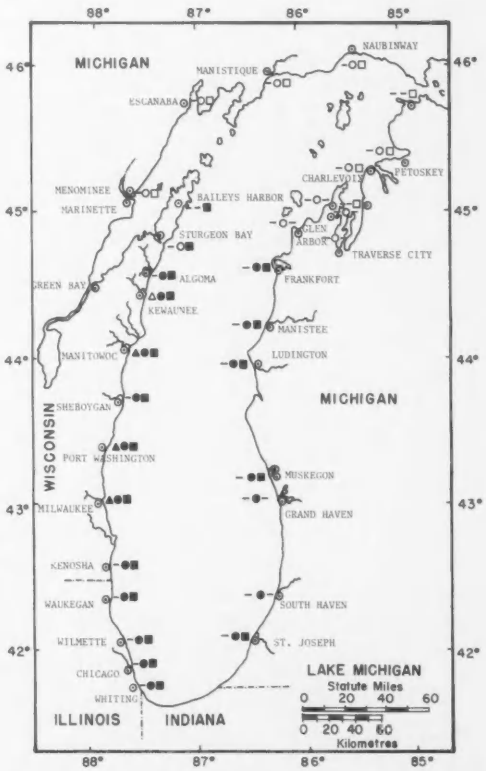

FIG. 1. Lake Michigan showing occurrence of *Bangia* along the lake shore observed from 1974 through 1976. Open symbols (△, ○, □) represent localities visited, closed symbols represent localities where *Bangia* growth was discovered, and hyphen (-) indicates no observation made. These symbols are arranged sequentially for the years 1974–76. △, 1974; ○, 1975; □, 1976.

typically germinate on substrates where they have lodged, to form young filaments. However, spores may remain and germinate in the parent cells, thus giving rise to masses of germlings (Fig. 2c).

The establishment of *Bangia* in Lake Michigan has caused vigorous competition with existing species for limited substrates. For example, where massive *Bangia* populations have developed, *Ulothrix zonata* (Weber and Mohr) Kütz. has been largely displaced. This is especially evident in the southern portions of the lake, and it may be principally in the cold months that the spores of *Bangia* establish the massive waterline populations. Sporelings have been seen growing epiphytically on *Ulothrix*. *Cladophora glomerata* usually attaches at or just below the waterline and has very durable holdfasts and basal akinetes; possibly because of this it is less threatened by *Bangia* than *Ulothrix* is.

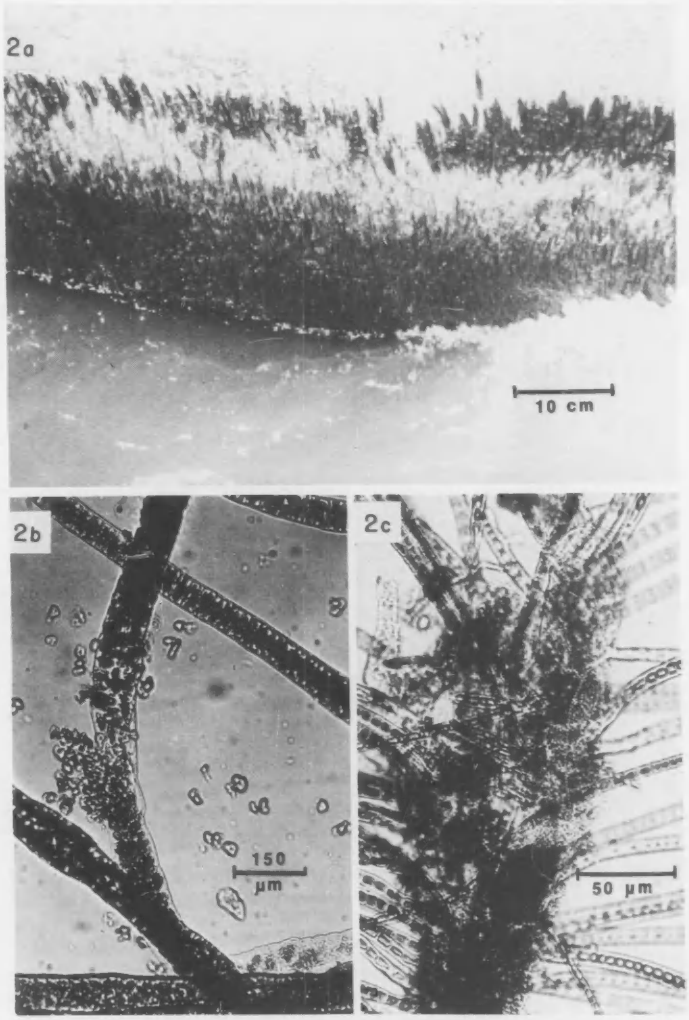

FIG. 2. a, Algal zonation on harbor breakwall along Lake Michigan shore. The upper dark band formed by *Bangia atropurpurea* appears purplish or reddish in nature and the lower dark band formed by *Cladophora glomerata* is dark green. Fluctuating water levels from 1.6 to 1 m may reach the lower parts of the upper band. b, Filament of *Bangia* showing monospore production. c, Filament of *Bangia* showing formation of new filaments from monospores that have remained and germinated in the parent plant.

Elemental composition — Like other red algae known to accumulate halogens in high concentrations (Shaw 1962) and to require a large variety of trace metals for normal growth (Provasoli et al. 1957), *Bangia* samples, collected from Grand Haven, Michigan, contain comparable high levels of some of these elements. Average values of triplicate samples in cellular composition (micrograms per gram dry weight algae) are I (12), Br (8532), Cl (1185), Co (28), Cu (287), Mn (181), Mo (267), Ru (1119), and Zn (4668). The high zinc content of *Bangia* may indicate a peculiar physiological requirement similar to that of *Porphyra tenera* (Noda and Horiguchi 1972). Likewise, Br and Cl, which occur in exceptionally high concentrations, are likely involved in unique and significant biochemical proces-

ses such as those possessed by many marine red algae (Fenical 1975). The present restriction of dense *Bangia* populations to harbor areas in Lake Michigan is possibly attributable to the tributary runoff such harbors often receive. Runoff was reported to be one of the principal sources of trace metals in Lake Michigan (Robbins et al. 1972). Meanwhile, rapid increases in Br and Cl concentrations in local inshore lake water are also reported (Tiffany et al. 1969).

Marine and freshwater entities of *Bangia* have often been considered as one species because of their similar morphology and euryhaline characteristics (Fritsch 1959). In fact, the marine entity *B. fuscopurpurea* can adapt successfully to fresh water under field and laboratory conditions (Hartog 1972; Geesink 1973), though the *Conchocelis* stage of the life history that commonly occurs in the marine entity has not yet been recorded in fresh water. *Bangia* species present in the North American Great Lakes have likely originated from coastal plants that migrated westward through the St. Lawrence Seaway. For the rapid invasion of a lake, e.g. Lake Michigan, transport by currents, aquatic animals, and ship hulls appear to be important dispersal mechanisms.

Previous evidence on migration and adaptation of marine organisms to the Great Lakes is well documented (Miller 1975; Robertson 1966). The rapid increase in complexity and quantity of chemical elements in nearshore water may enhance a trend toward the introduction of halophilic organisms in the Laurentian Great Lakes.

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The Yeast *Phaffia rhodozyma* as a Dietary Pigment Source for Salmonids and Crustaceans

ERIC A. JOHNSON

Department of Food Science and Technology, University of California, Davis, Calif. 95616, USA

DOUGLAS E. CONKLIN

Bodega Marine Laboratory, University of California, Bodega Bay, Calif. 94923, USA

AND MICHAEL J. LEWIS

Department of Food Science and Technology, University of California, Davis, Calif. 95616, USA

JOHNSON, E. A., D. E. CONKLIN, AND M. J. LEWIS. 1977. The yeast *Phaffia rhodozyma* as a dietary pigment source for salmonids and crustaceans. J. Fish. Res. Board Can. 34: 2417–2421.

The red yeast *Phaffia rhodozyma* contains astaxanthin as its principal carotenoid pigment. Incorporation of this yeast into the diet (15% wt/wt) of rainbow trout induced pigmentation within 43 days. However, lobsters fed the same diet did not readily accumulate the carotenoids of the yeast, though they became pigmented on a diet of live brine shrimp. The primary pigment isolated from the bodies of trout and lobsters fed the red yeast was astaxanthin. We conclude that *P. rhodozyma* is an excellent source of astaxanthin for cultivated salmonids.

Key words: astaxanthin, carotenoid, diet, lobster, *Phaffia rhodozyma*, salmonids, yeast

JOHNSON, E. A., D. E. CONKLIN, AND M. J. LEWIS. 1977. The yeast *Phaffia rhodozyma* as a dietary pigment source for salmonids and crustaceans. J. Fish. Res. Board Can. 34: 2417–2421.

La levure rouge *Phaffia rhodozyma* contient de l'astaxanthine comme principal pigment caroténoïde. L'incorporation de cette levure dans le régime alimentaire (15% du poids humide) de la truite arc-en-ciel déclenche la pigmentation en dedans de 43 jours. Cependant, les homards auxquels on donne le même régime n'accumulent pas facilement les caroténoïdes de la levure, quoiqu'ils deviennent pigmentés avec un régime d'artémies vivantes. Le pigment primaire isolé du corps des truites et des homards nourris à la levure rouge est l'astaxanthine. Nous concluons que *P. rhodozyma* est une excellente source d'astaxanthine pour les salmonidés d'élevage.

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AN important factor affecting the consumer acceptance of cultivated salmonids or crustaceans is the color of their flesh or carapace (Ostrander et al. 1976; Meyers 1977). The natural pink color of salmon flesh and the red color of boiled crustacean shells is due to the carotenoid astaxanthin (3,3′-Dihydroxy-β,β-carotene-4,4′-dione). In intensive culture systems for salmonids and crustaceans it is necessary to feed substances which contain astaxanthin to obtain this desirable pigmentation. Addition of 10–20% shrimp waste to fish diets is common practice in Norway (Hildingstam 1976). Crustacean shells, however, are low in protein and high in minerals which, without extensive processing to improve their dietary quality, restricts their inclusion in fish diets (Meyers 1977). Pigmentation of salmon and trout flesh has been accomplished using the synthetic carotenoid canthaxanthin (β,β,-Carotene-4,4′-dione) as a feed additive (Schmidt and Baker 1969), but this chemical is rather expensive (Hildingstam 1976) and does not produce a desirable color (Saito and Regier 1971).

Phaffia rhodozyma is a newly described yeast (Miller et al. 1976) which contains astaxanthin as its principal carotenoid (Andrewes et al. 1976). Depending upon the strain used and the growth conditions, the yeast contains 50–800 μg astaxanthin per gram of yeast (Johnson and Lewis unpublished data), which is about 10–30 times higher than most shrimp meals or crustacean products and approximately equal in content to krill or fish oils (Meyers 1977; Lambertsen and Braekkan 1971). Brewer's or baker's yeast is a highly nutritious component of fish

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diets (NRC/NAS 1973); *P. rhodozyma* has similar attributes and it provides the necessary carotenoid pigment; therefore it may be an ideal feed supplement for cultured salmonids and crustaceans. The present investigation was carried out to determine if astaxanthin from the yeast could be incorporated into the carapace of the American lobster, *Homarus americanus*, and the flesh of the rainbow trout, *Salmo gairdneri*.

Materials and methods — Feeding experiments — The two synthetic diets (Table 1) were identical except that one contained dried *P. rhodozyma* and the other dried brewer's yeast. The diets were prepared by mixing dry ingredients in a ball mill for 4 h, then adding oils and liquid ingredients, and blending for an additional 15 min. The mixed ingredients were combined with approximately 50% (by weight) of cold distilled water and kneaded to form a dough-like mass. This dough was extruded into pellets using a laboratory spaghetti extruder (Demarco 11 kg/h lab press) with a brass die with 2-mm orifices. After extrusion, these diets were air dried for 1 h and frozen for storage. Live brine shrimp (*Artemia salina*) were fed to the lobsters as a control diet.

One hundred and thirty-five juvenile 4th stage American lobsters (*Homarus americanus*) were randomly divided into three diet groups in a closed artificial seawater system described by Hand (1977). The system contained Instant Ocean (Aquarium Systems Inc.) and salinity was maintained at 33‰. Water temperature was 21°C for the 60-day feeding period. Lobsters were fed once a day in the afternoon. Before each feeding, uneaten food was removed by siphon. Carapace length (to the nearest 0.1 mm) and wet weight (to the nearest 1.0 mg) were determined on the 10th day and on the final day of the feeding trial.

Fifty rainbow trout (*Salmo gairdneri*), Mt. Whitney Strain, approximately 9 mo old, were obtained from the Nimbus Hatchery, State of California Department of Fish and Game. Fish were randomly distributed into two stainless steel tanks each holding 245 ℓ of water, to which fresh water was continuously added at a rate of 45 ℓ/h. The tank water was pumped through 25-μm cartridge filters by submersible pumps. Water temperature was held at 15.5°C and aeration was provided with airstones. Fish were fed approximately 2% of their body weight each day, divided into three feedings, of diets 1 and 2. Samples of fish were taken at 14, 19, 37 and 43 days, and were frozen at −20°C for later analysis.

Extraction of carotenoids from lobsters and fish — Lobsters from each diet group were boiled for 3 min and photographed. The animals were then frozen and freeze-dried. The dried lobsters from each group were pooled and homogenized in a Waring blender with 100 ml acetone and 50 ml 0.5-mm glass beads under an N_2 atmosphere. The lobster–acetone mixture was filtered and the lobster debris was then reextracted twice with 100-ml portions of acetone. The extracts were combined for analysis.

The frozen trout were skinned and photographed. The filets were then freeze-dried, weighed, and crumbled into 500-ml flasks. Approximately 150 ml acetone was added and the flasks sealed under nitrogen. The mixture was shaken at 200 rpm at 7°C for 2 h and filtered. The meat residue was ground with sand and reextracted with acetone until the debris was colorless. The extracts were combined.

TABLE 1. Composition of diets 1–3 (% dry weight basis).

Ingredient	Diet 1	Diet 2	Diet 3
Casein (purified, hi-nitrogen)[a]	15.8	15.8	—
Albumin (egg)[a]	2.0	2.0	—
Mineral mix[h]	2.5	2.5	—
Wheat gluten[a]	10.0	10.0	—
Corn starch[a]	10.0	10.0	—
Alphacel[a]	35.49	35.49	—
Choline chloride[a]	0.7	0.7	—
Vit mix C[h]	2.0	2.0	—
Cholesterol[d]	0.5	0.5	—
Ethoxyquin[g]	0.022	0.022	—
Cod liver oil[a]	3.78	3.78	—
Corn oil[a]	1.98	1.98	—
Vit E acetate[e]	0.228	0.228	—
Dried brewer's yeast[b]	—	15.0	—
Phaffia rhodozyma[c]	15.0	—	—
Live brine shrimp[f]	—	—	100

[a]ICN Pharmaceuticals, Inc., Cleveland, Ohio.
[b]Yeaco 20, Millbrew, Inc., Juneau, Wis.
[c]Food Science and Technology Yeast Collection (UCD 67-210), University of California, Davis, Calif.
[d]General Biochemicals, Chagrin Fall, Ohio.
[e]Roche Chemical Division, Nutley, N.J.
[f]Metaframe Corporation, Oakland, Calif.
[g]"Santoquin," Monsanto Agricultural Products Company, St. Louis, Mo.
[h]See Conklin et al. (1977).

The acetone extracts of lobsters (all diets) and fish (diet 1) gave an electronic absorption spectrum typical of astaxanthin, and the known spectral characteristics of $E^{1\%}_{1cm}$ = 1600 and λ_{max} = 478 nm in acetone (Andrewes et al. 1976) were used in the calculation of pigment concentration. However, the acetone extract of the fish fed diet 2 gave an absorption spectrum with a λ_{max} of 453 nm which is due to an unknown pigment probably from previous diets; for comparison the same specific extinction coefficient of $E^{1\%}_{1cm}$ = 1600 was used in the calculation. The carotenoids were transferred to petroleum ether, dried over sodium sulfate, and the solutions evaporated to dryness under reduced pressure.

Purification of carotenoids — Pigment extracts were initially chromatographed by thin-layer chromatography on silica gel (Silica Gel 60, 0.25 mm thickness, Brinkmann Instruments Inc.) using 15% acetone in petroleum ether. The main carotenoid from each group of animals was further purified by chromatography on thin-layer and silica-impregnated paper using acetone–petroleum ether solvent mixtures. All carotenoid manipulations were performed in dimmed lighting at room temperature and protected from air.

Electronic absorption spectra were recorded on a Cary 15 instrument. The mass spectra were determined on a Finnegan 3200 instrument at 230°C with ionization voltage 70 eV.

Yeast growth — Phaffia rhodozyma was grown for 60 h at 23°C with air flow rate of 50 ℓ/min and vigorous stirring (4000 rpm) in 60-ℓ fermentors in a liquid medium containing per litre: cerelose, 20 g; $(NH_4)_2SO_4$, 2.0 g; KH_2PO_4, 1.0 g; yeast extract (Difco), 2.0 g; and buffered with 1% (vol/vol) lactic acid adjusted to pH 4.5 with KOH. The cells were harvested in a Sharples continuous centrifuge, shaken with glass beads for 2 min in a Braun tissue disintegrator, and freeze-dried for diet preparation.

Results — Lobster growth and pigmentation — Lobsters fed live brine shrimp (diet 3, Fig. 1) had greater length and weight increase than lobsters fed either of the yeast diets (Student–Newman–Keuls Multiple Range test, $\alpha = 0.05$), whereas the two yeast diets supported equal weight gain and increase in carapace length. Approximately 90% survival was observed for all three groups of lobsters.

Lobsters fed brine shrimp contained more carotenoid than lobsters fed yeast diets (Table 2). Lobsters fed diet 1, containing *P. rhodozyma*, had more carotenoid than lobsters fed diet 2 (white yeast). As expected, the red color was judged visually of the boiled lobsters correlated with their carotenoid content.

Trout growth and pigmentation — Rainbow trout fed yeast diets increased their mean body weight by a factor of 1.5 during the 43-day feeding. Both fish groups readily accepted the synthetic diets. Those fed diet 1 showed rapid astaxanthin accumulation over the 43 days (Fig. 2). Fish fed the white yeast diet decreased in carotenoid content and their flesh showed no visible pigmentation at the end of the test period. The linear regressions for the two sets of data (Fig. 2) are significantly different ($\hat{\beta}_2 = -0.0860, \hat{\beta}_1 = +0.1621, t = 4.68$ df $= 4, \alpha = 0.05$).

TABLE 2. Carotenoid content of diets and lobsters (expressed on a dry weight basis in micrograms per gram).

	Diet		
	1	2	3
Total carotenoid content of the diet	52.2 (30.7)[b]	0 (0)[b]	90.0[a] —[c]
Carotenoid content of the lobsters	80.9 (139.4)[d]	54.7	130.2

[a]Estimated as canthaxanthin ($\lambda_{max} = 463$ in petroleum ether, $E^{1\%}_{1cm} = 2200$). (Davies 1976).
[b]Total carotenoid content after 5 mo storage at 0°C.
[c]Brine shrimp received fresh weekly; 90.0 μg/g is the mean of two extractions.
[d]Estimated carotenoid content assuming diet 1 equal in carotenoid content to diet 3.

Identification of carotenoids — The primary carotenoid (>85% of the total present) isolated from the three groups of lobsters and the fish fed diet 1 was chromatographically and spectrophotometrically identical with pure astaxanthin isolated from *P.*

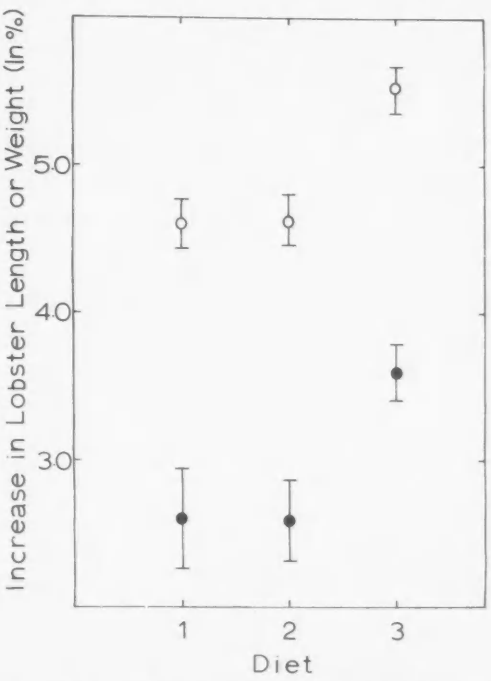

FIG. 1. Change in lobster carapace length (●—●) or wet weight (○—○). Expressed as $\log_e$ (% increase).

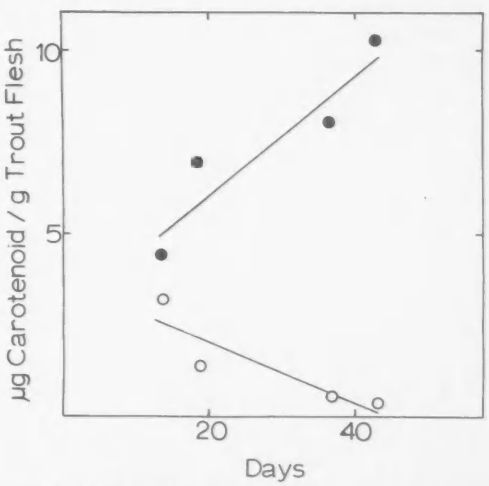

FIG. 2. Carotenoid content of rainbow trout fed diet 1 (●—●) or diet 2 (○—○).

rhodozyma. The visible spectra of the pigment from the four sources were identical (λ_{max} = 478 nm in acetone) and typical of astaxanthin (Davies 1976). The mass spectra of astaxanthin from the fish and from the yeast gave identical molecular ions (M^+ = 596) and similar fragmentation patterns. The primary carotenoids from each group were chromatographed with each other and with yeast astaxanthin in two systems: (1) silica gel TLC, R_f = 0.12, 15% acetone in petroleum ether; (2) Kieselguhr impregnated paper (Schleicher and Schuell no. 287), R_f = 0.39, 10% acetone in petroleum ether. The identity of astaxanthin from the three groups of lobsters and from the fish fed diet 1 was confirmed. The amount of carotenoids present in fish fed diet 2 was insufficient to allow identification.

Discussion — The red color of wild salmon and rainbow trout is due primarily to the carotenoid astaxanthin, which occurs unesterified in the muscle of these fishes (Kanemitsu and Aoe 1958; Hata and Hata 1975). In nature, the consumption of crustaceans and insects is responsible for the accumulation of astaxanthin (Fox 1957; Steven 1947). In our study astaxanthin from the yeast *P. rhodozyma* was incorporated in salmonid flesh at a rate faster than reported for dried crustacean waste (Saito and Regier 1971). The yeast *P. rhodozyma* is therefore a promising commercial source of astaxanthin in the cultivated salmonid industry.

Lobsters fed *P. rhodozyma* did not accumulate as much carotenoid as the lobsters fed live brine shrimp (Table 2). The primary carotenoid in brine shrimp is canthaxanthin (Krinsky 1965), which needs to be transformed into the astaxanthin of the lobster carapace. In fact, canthaxanthin is postulated to be an intermediate in the transformation of β-Carotene to astaxanthin in the lobster *Panulirus japonicus* (Katayama et al. 1973). Direct feeding of yeast containing astaxanthin would be expected, therefore, to enhance accumulation of carotenoids by the lobster, but this was not observed in this study.

Lobsters fed *P. rhodozyma* did show greater pigmentation than lobsters fed the control diet, but the carotenoid content of the lobsters was relatively low. This may be due to meager consumption of the pelletized diet as reflected in the poor growth of the animals. Another possible explanation for less carotenoid accumulation in the lobsters fed *P. rhodozyma* concerns the stereochemistry of the astaxanthin molecule. Astaxanthin present in the yeast has the 3R, 3′R configuration (Andrewes and Starr 1976), which is the opposite configuration of astaxanthin obtained from other sources (Veerman et al. 1974); the interesting possibility arises that the yeast astaxanthin cannot be a component of the carotenoprotein crustacyanin because of its configuration. If this is the case, the accumulation of carotenoids in lobsters fed *P. rhodozyma* may be due to the slower utilization of carotenoids found in lower concentrations in the yeast, e.g. echinenone (β,β-Caroten-4-one).

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Dinoflagellate Toxins as Probable Cause of an Atlantic Herring (*Clupea harengus harengus*) Kill, and Pteropods as Apparent Vector

ALAN W. WHITE

Department of Fisheries and the Environment, Fisheries and Marine Service, Biological Station, St. Andrews, N.B. E0G 2X0

WHITE, A. W. 1977. Dinoflagellate toxins as probable cause of an Atlantic herring (*Clupea harengus harengus*) kill, and pteropods as apparent vector. J. Fish. Res. Board Can. 34: 2421–2424.

Stomachs of Atlantic herring (*Clupea harengus harengus*) from a kill that occurred in the Bay of Fundy during a bloom of the toxic dinoflagellate *Gonyaulax excavata* contained pteropods, algal remains, and paralytic toxins. Experiments show that comparable amounts of *G. excavata* toxins can kill herring rapidly. It is likely that the kill was caused by paralytic dinoflagellate toxins, and that the pteropod *Limacina retroversa*, a planktonic herbivore, acted as a vector of the toxins.

Key words: Dinoflagellate toxins, *Gonyaulax excavata*, herring kill, *Clupea harengus harengus*, pteropod, *Limacina retroversa*

WHITE, A. W. 1977. Dinoflagellate toxins as probable cause of an Atlantic herring (*Clupea harengus harengus*) kill, and pteropods as apparent vector. J. Fish. Res. Board Can. 34: 2421–2424.

Les estomacs de harengs atlantiques (*Clupea harengus harengus*) prélevés au cours d'une mortalité qui se produisit dans la baie de Fundy à la suite de fleurs d'eau du dinoflagellé toxique *Gonyaulax excavata* contenaient des ptéropodes, des restes d'algues et des toxines causant la paralysie. Des expériences démontrent que des quantités comparables de toxines de *G. excavata* peuvent rapidement tuer les harengs. Il est probable que la mortalité fut causée par des toxines du dinoflagellé, et que le ptéropode *Limacina retroversa*, un herbivore planctonique, agit comme vecteur des toxines.

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THE toxic dinoflagellate causing paralytic shellfish poisoning (PSP) in eastern Canada, New England, and northeastern England is *Gonyaulax excavata*, formerly *G. tamarensis* (Loeblich and Loeblich 1975). The effects of its toxins on warm-blooded animals are well known (Prakash et al. 1971). However, there is little information regarding the fate and consequences of its toxins in marine food chains, or the susceptibility of marine organisms to them (Prakash et al. 1971; Caddy and Chandler 1968; Yentsch and Balch 1975; Gilfillan and Hanson 1975). Although not previously established, it is reasonable that planktonic herbivores may act as vectors of the toxins. Adams et al. (1968) described a mass mortality of sand eels and sea birds along the northeast coast of the United Kingdom that may have been the result of toxins acting through a food chain of *G.*

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tamarensis (*excavata*)–planktonic herbivores–sand eels–sea birds. This paper discusses a herring kill probably caused by *G. excavata* toxins which had likely been accumulated by pteropods, and presents evidence that the toxins are lethal to herring. This is the first report implicating a toxic dinoflagellate in a fish kill on the northeast coast of North America.

Materials and methods — On July 15, 1976, an Atlantic herring (*Clupea harengus harengus*) kill occurred in the Bay of Fundy from about White Head to North Head (≈16 km) off the coast of Grand Manan Island (44°43′N, 66°48′W). Samples of dead or dying herring were collected from the site of the kill, iced, and transported to the laboratory within a few hours. Surface water temperatures at the time of the kill were 11–12°C.

Pigment analysis of the yellow-brown material in the herring stomachs and pteropods was conducted fluorometrically on 90% acetone extracts by the method of Yentsch and Menzel (1963).

Measurements of paralytic dinoflagellate toxins were made according to the standard mouse bioassay for shellfish investigations (AOAC 1975). Whole stomachs (and contents) of 40 herring from the kill were homogenized and extracted with 0.1 N HCl as described in the method. The extract was adjusted to pH 3.4 and sent to the Department of National Health and Welfare in Ottawa, where "10-mice" bioassays were conducted.

For experiments on the effects of *G. excavata* toxins, crude toxin extracts were prepared by harvesting mass, bacteria-free cultures of the dinoflagellate by gentle centrifugation and boiling the cells for 5 min in 0.1 N HCl. The amount of toxins in the extract was determined by "10-mice" bioassays as above. Herring were collected locally and maintained in the laboratory for several weeks on a diet of brine shrimp. Experiments were conducted on three separate dates during the winter. Water temperatures were 2.5–3.0°C. Twenty-one micrograms of toxins in 0.2 ml of extract (adjusted to pH 2.0) was injected directly into the herring's stomach with a 14-gauge 10-cm, blunted needle passed down the throat. Tests using food coloring showed that a considerable amount of extract could be regurgitated in the first few minutes. Twenty-eight control fish in the same size range as treated fish were injected with 0.2 ml of 0.01 N HCl (pH 2.0).

Results and discussion — In the Bay of Fundy on July 15, 1976, mature herring, 20–26 cm total length (65–150 g estimated weight), were observed dead and dying, many with widely gaping mouths, in patches at the surface. It was learned subsequently that a similar herring kill had occurred along the nearby coast of Maine on July 10.

Dumping of excess fish by a purse seiner was an unlikely cause of the kill because few scales were missing from the dead fish. The possibility that the kill was caused by military practice bombing (the site is near a designated practice bombing area) was also ruled out because X-ray examinations showed no lateral displacement of vertebral columns, and no internal hemorrhaging or aberrations of organs or tissues were observed. No parasites or associated abnormalities were detected in the dead herring. Unfortunately, tests for pathogenic microorganisms were not conducted.

Stomach contents were examined. The stomachs were only partially full (≈0.3 g contents per stomach), and the contents were almost entirely composed of thecosomatous pteropods identified by their shells (1–2 mm in height) as *Limacina* (*Spiratella*) *retroversa* forma *retroversa* (van der Spoel 1972). Several dozen pteropods in various stages of digestion were found in most stomachs along with a yellow-brown material consisting of chromatophore-like bodies also in various stages of digestion. This material was present inside the pteropods as well, and probably represented the remains of the algae on which the pteropods had been feeding. The algal nature of the material was verified by pigment analysis, which revealed the presence of a small amount of chlorophyll *a* and large amounts of phaeopigments (chlorophyll degradation products).

The levels of paralytic toxins in shellfish (*Mya arenaria*, *Mytilus edulis*, *Modiolus modiolus*) in the southwestern Bay of Fundy had been increasing rapidly during the first 2 wk of July. Also, phytoplankton net tows (20 μm mesh) made on the day of the herring kill in the same general area (between Grand Manan Island and Campobello Island) showed the presence of a very large number of the toxic dinoflagellate *Gonyaulax excavata*; it was certainly the most dominant phytoplankter in the area at that time. These findings, along with those already mentioned, led to the hypothesis that the herring had died from PSP, as a result of eating pteropods that, in turn, had fed on *G. excavata* and accumulated its toxins.

Accordingly, the herring were assayed for paralytic dinoflagellate toxins. Results were positive. Duplicate tests measured 1446 and 1382 μg of paralytic toxins per 100 g of stomach tissue and contents, i.e. about 21 μg per stomach. Toxins were undetectable by the bioassay in fillets of five herring, i.e. <34 μg of toxins per 100 g of meat.

Certain dinoflagellates are known to produce toxins that can kill fish and have been associated with fish kills and mass mortalities of marine animals, such as *Gymnodinium breve* and *Gonyaulax monilata* in the Gulf of Mexico (Gates and Wilson 1960; Wilson et al. 1975; Wardle et al. 1975). However, little is known about the effects of toxins from *Gonyaulax excavata* on fish and most other marine organisms. It has been suggested that cold-blooded vertebrates may be relatively insensitive to these toxins (Prakash et al. 1971).

Therefore, experiments were conducted to determine the effects of *Gonyaulax excavata* toxins to herring. Table 1 summarizes the results when 21 μg of toxins (the amount per stomach in fish from the kill) was administered as a crude extract directly to the fish's stomach. Because preliminary experi-

TABLE 1. Effect of *Gonyaulax excavata* toxins on herring. Paralysis is time at which fish was immobilized and lay on its side at bottom of tank.

Herring wt (g)	Total length (cm)	Time after treatment	
		Until paralysis (min)	Until death (min)
10.6	12.8	12	110[a]
11.1	13.1	10	75[a]
11.1	12.8	11	60
11.4	13.1	8	80
11.6	12.7	11	43
11.6	13.4	11	60
11.7	13.0	9	42
12.0	13.1	9	58
12.2	13.1	15	110[a]
12.3	13.4	10	54
12.3	13.2	13	98[a]
12.3	14.2	20	—[b]
12.7	13.1	19	140
12.9	13.7	15	—[b]
13.5	13.6	7	37[a]
13.5	13.6	9	75[a]
13.8	14.1	12	—[b]
14.5	14.1	16	—[b]
14.6	14.1	16	150[a]
14.6	13.7	20	—[b]
15.0	13.7	7	51
15.6	14.0	15	100[a]
15.6	14.8	11	105[a]
16.0	14.5	10	51
17.3	14.7	14	420–1500[a]
17.9	14.8	14	49
18.2	15.2	loss of equilibrium only	—[b]
20.4	15.0	18	120[a]

[a]Fish died with mouth gaping widely.
[b]Fish normal 48 h after treatment.

ments using food coloring showed that fish could regurgitate and lose substantial amounts of extract in the first few minutes, 21 μg of toxins was the nominal dose; the actual effective dose was probably considerably less.

The results show clearly that *Gonyaulax excavata* toxins can be lethal to herring. All 28 treated fish displayed similar symptoms within several minutes after treatment. Initially, fish swam in an irregular, jerky manner, and soon after lost their equilibrium and swam on their sides. Floating on the surface was observed in several instances. In all fish except one paralysis occurred within 10–20 min after treatment to the degree that the fish became immobilized on the bottom of the tank, breathing either very slowly and weakly or only in sporadic gasps. Occasionally, fish in this condition swam wildly in tight circles for very short periods. (Mullet show symptoms resembling these when exposed to *G. monilata* (Gates and Wilson 1960)). Twenty-two of the 28 treated fish died (79% mortality), all except one within 1 or 2 h after treatment. One half of these fish died with their mouths gaping widely, as was noted in many fish from the kill, indicating asphyxiation as the probable cause of death. The six fish that survived the toxin treatment resumed erratic swimming after several hours and resumed normal swimming on the following day; they survived for 48 h when observations were terminated. All 28 control fish survived for 48 h and showed no abnormal behavior.

The fish used in these experiments were smaller than those from the kill. Also, the experiments were conducted in the winter when the water temperature was only 2.5–3.0°C. It is reasonable that since 21 μg of toxins (and probably much less because some was regurgitated) is sufficient to kill herring 10–20 cm long at low temperatures, that a similar amount is sufficient to kill herring 20–26 cm long in the summer when water temperatures are 11–12°C and the fish are metabolically more active.

In conclusion, this study strongly suggests that the herring kill off Grand Manan in 1976 was due to paralytic toxins from the dinoflagellate *Gonyaulax excavata*. Additionally, it is reasonable that the pteropod *Limacina retroversa* acted as a vector of the toxins because of the following evidence: (1) pteropods were the only major item in herring stomachs besides degraded algal material, (2) the pteropods, which are planktonic, mucilaginous filter-feeders, contained degraded algal material, (3) *G. excavata* was the dominant phytoplankter at the time of the kill, (4) pteropods are molluscs and may well be able to accumulate dinoflagellate toxins as do many bivalve shellfish, and (5) mature herring are not known to ingest phytoplankton directly.

Similar repercussions involving other components of marine food chains may occur during blooms of *G. excavata*, especially during "bad" blooms as in the summer of 1976. There is a need to test the effects of these toxins on other cold-blooded marine organisms and to determine the fate and consequences of the toxins in marine systems.

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Nomenclatura Oligochaetologica: A Catalogue of Names, Descriptions and Type Specimens of the Oligochaeta. *J. W. Reynolds and D. G. Cook. University of New Brunswick, Fredericton, N.B., 1976. x + 217 p. $15.00.*

At first impression this book has something of the air of a limited private edition; the quality of the production, the use of Latin, and the pleasing if somewhat archaic use of the final page colophon all lend themselves to divorcing this book from the great mass of more mundane scientific texts. All very pleasing, but I think that one of these attributes should be questioned a little: the use of Latin for chapter and section headings throughout the book.

Latin is no longer the international common scientific language that it may have been in earlier stages of western scientific development, as proved by the use of six different languages in this book. The use of Latin has persisted only in botanical descriptions and in the construction of various zoological names, particularly, of course, at the generic and specific levels. Therefore, at the risk of being chauvinistic about my own tongue, I feel that English is the only possible candidate for the role of a global scientific language and that the use of English headings in this book would have simplified finding one's way around. It may be easy for anyone who speaks a Romance language to guess the meaning of, for example, 'Index Auctoritatum," but why should we have to guess? However, this is not to be regarded as a serious fault and it in no way detracts from the essential worth of the book — petty carping is an occupational hazard of the book reviewer and it is an unfortunate fact that adverse criticism generates greater verbosity than does praise, no matter how well deserved.

The scope of this book is admirably summed up by the alternative title "A Catalogue of Names, Descriptions and Type Specimens of the Oligochaeta." It is satisfying to find a book that lives up to the promise of the title and a title that renders superfluous any further description of the contents. This standard of quality is maintained in all aspects of the book and a few points are worthy of particular mention.

First on my list is the use of more than one language. Science in general and taxonomy in particular always seems to claim for itself an international status which is so often denied by the parochial and nationalistic attitudes of much scientific writing. The authors are therefore to be particularly commended for their use of six different languages, English, French, German, Russian, Portuguese, and Chinese in the crucial "how to use this book" section. Of course, this catalogue type of book lends itself particularly well to this approach; other more descriptive texts would presumably be impossible to handle in this manner. However, the ease of execution in this instance in no way detracts from the truly cosmopolitan outlook of the authors. Praise is due for the choice of Chinese rather than Japanese for the oriental language; it seems to be an unfortunately widespread occidental misconception that Japanese is the more widely used and understood of the two. I have slight doubts about the choice of Portugese rather than Spanish. Personally, I would consider Spanish to have the larger potential audience, but considering the high degree of mutual comprehension between these two languages, I am confident that no real problem exists.

Another pleasing point is the authors' decision to list names strictly alphabetically rather than in any kind of systematic hierarchy. This simple and practical decision enhances and extends the useful life of the book since no change in the systematic arrangement of the Oligochaeta, no matter how superficial or fundamental, can now detract from the function of the book. The temptation to impose their own views of oligochaeta systematics must at times have been overwhelming to the authors, so this note of restraint and conservatism is particularly welcome in a field that has occasionally suffered excessively from premature enthusiasm.

I don't know who decided upon the actual physical construction of the book, but the publishers and/or the authors are to be thanked for choosing a substantial grade of paper and a satisfactorily solid binding; reference works of this caliber should be built to withstand the rigors of both desk and laboratory bench; this one is, many are not.

In general this is a comprehensive, well-researched, and excellently presented book. It may be somewhat limited in its audience — oligochaetes are, after all, still a rather esoteric study — but its usefulness will be enormous both to those in the field and those whose interest is more peripheral. After the slough of confusion into which oligochaete systematics had fallen in the middle of this century, it is gratifying to witness a strong recovery of the discipline exemplified firstly by the book of Brinkhurst and Jamieson (1971), and now by this essential handbook by Reynolds and Cook.

J. R. PICKAVANCE

Department of Biology
Memorial University
St. John's, Newfoundland A1C 5S7 (R168)

BRINKHURST, R. O., AND B. G. M. JAMIESON. 1971. Aquatic Oligochaeta of the World. University of Toronto Press, Toronto, Ont. xi + 860 p.

Recovery and Restoration of Damaged Ecosystems. *Edited by J. Cairns Jr., K. L. Dickson, and E. E. Herricks. The University Press of Virginia, Charlottesville, Va. 22903, USA, 1977. x + 531 p. $20.00.*

This is an ambitious book. It attempts to deal with ecosystems from the arctic to the tropics and a variety of ecological disasters: oil spills, fire, strip mining, eutrophication, permafrost destruction, tropical land use, urban decay, and toxic chemical spills. The format of most papers is simple: the structure of the perturbed ecosystem is described and the return to the original structure at various times after the perturbation has been removed are detailed.

Edmondson's paper on the recovery of Lake Washington following nutrient diversion is the best example of these papers; it is concise and the implications for the recovery of other lakes are clear. Most of the other papers are stuffed with species lists, chemical data, and qualitative descriptions that are difficult to digest. To someone interested in a specific subject an individual chapter might be a useful introduction to the literature but it was a mistake to put them consecutively in a book — nothing sticks at the end. It is like an uncoordinated musical group — everyone is technically competent with his own instrument but none communicate so there is no music. The problem is not with the musicians, it is with the conductor — it was a mistake to try to include such a broad array of topics in a single volume. The conference could have been usefully devoted to a single problem area — oil spills, for example — where a common problem would bind the contributions together. As it is, the problems are so different that nothing carries over from one paper to the next, and the book as a whole is tedious.

EVERETT J. FEE

Department of Fisheries and the Environment
Fisheries and Marine Service
Freshwater Institute
Winnipeg, Man. R3T 2N6 (R159)

Herbicides: Chemistry, Degradation and Mode of Action. *Edited by P. C. Kearney and D. D. Kaufman. 2nd ed., revised and expanded. Marcel Dekker, Inc., New York, N.Y., 1976. Vol. 2. xi + 501–1036. $47.50 U.S.*

Herbicides form a major portion of pesticides used in Canada, particularly in southern Ontario and Quebec and on the Canadian prairies. While the permitted uses of these herbicides are predicated on environmental compatibility and safety, levels of herbicides of undesirable proportions may still enter Canadian waterways through misuse, overuse, or accidental spills. Kearney and Kaufman's second edition, volume two, especially when combined with volume one, is a valuable reference for anyone connected with research, teaching, or policy making in the area of herbicide use, degradation, mode of action, and environmental fate.

Kearney and Kaufman's first edition, *Degradation of Herbicides*, published in 1969, quickly became the authoritative reference text in this field. The gathering of information on herbicide degradation into one concise book had not successfully been attempted previously. The second edition not only provides a timely update to a respected work, it also includes new chapters in areas not covered in the first edition. Whereas volume one is composed almost entirely of topics that had been discussed in the first edition, volume two is about 60% new material in the sense that the topics were not discussed in the first edition. As a result, the two-volume second edition presents a much more complete picture of the chemistry, degradation, and mode of action of herbicides as they are available today.

The book is a series of comprehensive review articles written by recognized authorities in individual fields. Chapters carried forward and updated from the first edition describe dipyridyls, benzoic acids, methyl and phenyl carbamates, and herbicide photodecomposition. New sections deal with phenols, diphenyl ethers, organoarsenicals, picloram and related compounds, acylanilides, miscellaneous herbicides, and herbicide volatility. Some chapters include comments on related insecticides, e.g. methyl carbamates and organoarsenicals, and the photochemistry and volatility chapters contain much of value to workers both inside and beyond the herbicide field.

The book is well organized with a consistent format used throughout, modified only as required to accommodate the completeness of the scientific literature. Other features appreciated by this reviewer were the extensive subject and author indexes for both volumes at the end of volume 2, indications of gaps in the literature both directly and by implication, and the grouping of data on herbicide degradation in plants, animals, and soil in one place. The chapters on photochemistry and volatility are especially valuable since these phenomena are so important in the loss and destruction of herbicide residues. It is a pity that a chapter on adsorption was not included; however, this field has received relatively good coverage elsewhere.

Although the updated chapters have been well reworked, and, in several instances, have been rewritten by new authors, these and the new chapters all too frequently cover literature only to 1972. More recent references, where cited, in many instances are from the authors' own laboratories or are unpublished data. Although this is not the first time, nor will it be the last, it is a pity that it required so long a time to go from the writing of the chapters to the publishing of the book. Perhaps it is because of this dating of the book that notable herbicides such as asulam, benazolin, benzoylprop, ethyl, difenzoquat, glyphosate, and vapam are not included.

By nature, the chapters are complete unto themselves, and little or no cross referencing is required; however, DCPA (dimethyl tetrachloro terephthalate) is discussed in two chapters, as a benzoic acid (where it belongs) and again as a miscellaneous herbicide. There is so little material in either place that it is surprising that the editors did not see fit to combine these two sections. In this case, cross referencing would have been useful. A second herbicide discussed as a miscellaneous herbicide which belongs more suitably in the benzoic acid family is naptalam. Fortunately, the subject index is present for those interested in herbicides of ambiguous parentage.

The miscellaneous herbicide chapter is perhaps the most difficult and frustrating to write because of the sketchy information available for these compounds in the literature. However, it is disturbing that, of the eleven compounds discussed in this chapter, three are given incorrect structures; viz. bensulide and naptalam in Table 1, and dazomet in Figure 1.

Volume two is very readable and suitable for the intended readership, i.e. scientists, students, and administrators; however, the discussion of the gas saturation method for vapor pressure determination in Chapter 19 is difficult to follow since the text and the accompanying diagram do not correspond, and the expression derived for saturation pressure is confusing. The book is otherwise of high quality and well worthwhile to provide the reader with a comprehensive background in herbicide chemistry and biochemistry. Because of its price, however, this book is most likely to be owned by libraries and institutions rather than by individuals.

G. R. BARRIE WEBSTER

Pesticide Research Laboratory
Department of Soil Science, University of Manitoba
Winnipeg, Man. R3T 2N2 (R130)

Farming the Edge of the Sea. *E. S. Iversen. Fishing News Books, Ltd. Farnham Surrey, England. 436 p., 202 illus., 17 tables. £13.50*

This updated version of the 1970 original still has the purpose of being "a general integrated summary of sea farming and the state of the art (of it?), primarily in developed countries."

Iversen succeeded reasonably well in achieving this purpose. The book is semipopular with the occasional lapse into scientific terminology, perhaps too much of it for real laymen, but it gets its message across. As interpreted by me the message reads: Farming the edge of the sea has succeeded here and there; it can succeed in still more sites. It is a risky business, classified by insurance firms as "high risk venture," but it is a business and one engages in it to make money. That one also supplies delicious morsels of protein, valuable industrial colloids, condiments, pearls, etc. in the process is important but one's desire to do so is only the beginning of doing marine and brackishwater aquaculture. There could even be more emphasis on the economic, legal, and regulatory aspects than there is, even though the author has added a new chapter on economic feasibilities. He falls a little short in stressing the need to seize all possible amenities that save fixed and running production costs such as warmwater effluents, trashfish for the feed of carnivores, etc., and that economies of scale, especially in labor, prevail prominently in aquafarms of developed countries.

One of the rationales for doing aquaculture along the edge of the sea the author says, is to even out supplies of sea food. That aquaculture hardly begins to do so remains a good reason for pushing on with removing some biotechnical obstacles to sea farming. The first and foremost of those obstacles are low larval survival and control over reproductive physiology of several fish and invertebrates potentially popular for culture that have very small eggs, like most of their kind. Improvement of those skills will allow us to do a lot more "improvement through artificial selection" (a chapter heading of the book) and hopefully put marine animals near the ball park, one day, now occupied by chickens or pigs.

Iversen starts out with two chapters of a very general nature; one is a rationale for pursuing sea farming altogether and the other a historical overview. Both are brief and therefore contain only the broadest information. I am glad he ends his beginning with the caution that "sea farms, even if increased substantially, will not greatly affect production for sea fisheries; it will be a fraction of that produced by fishing."

Next follow three chapters on methods dealing with sites, ponds, enclosures, feeds, feeding, and fertilizing and selective breeding. It is strongly stressed that our knowledge of genetics of aquatic animals is rudimentary. What is more, we have reason to suspect that some fishes may be far more prone to yield substantial results from practical breeding endeavors than others. The trout and salmon family may well be such a group.

We then proceed to the third set of chapters that deal with presently farmed species in some detail and end with a potpourri of comments on invertebrates and vertebrates that may have potential for farming. These last two chapters bring home forcefully that some trails are just not worth pursuing (spiny lobsters), and that successful aquacultural business ventures can produce all sorts of commodities such as worms for bait. Somewhere here the subject of sea ranching is touched upon briefly, and the reader is told rightly that this must be a government activity as the fishery for the fish that return needs to operate on the basis of harvesting a common property.

The book ends with two sections, one on diseases, predation, etc., and pollution as well as site competition and regulations now hedging in the farmer on the edge of the sea, and the other on economics topped off with a checklist that repeats in a nutshell what the book has said all along. Its intent is to serve as guide to the lucky person with funds to invest, the desire to grow aquatic organisms, plenty of business acumen and management skills, and a boundless proclivity for hard work.

I greatly respect the author for his constant admonition to dig for more details in the scientific literature and I sympathize with him for obviously not having wanted to give so many areas the light onceover (e.g. diseases), but I respect him for having drawn the line. There are few places where the update could have been more complete but then aquaculture is a very fast growing field and I for one know very well that a critic can always pick some nits on this score. The "edge of the sea" is rather broadly defined and species are included one does not usually associate with the sea — tilapia, catfish, trout. One should, though, for I have caught fine large tilapia in closed lagoons with 40‰ salinity; catfish can be grown in brackish water; and trout thrive in half strength seawater.

As much as I like the book, it has a slight "technical journal" cast of writing, perhaps too much so for its purpose. I am still hoping and waiting for the truly popular book on aquaculture that does not tout the enterprise as a panacea, but that informs one fully and that can be used from high schools anywhere to ministries of planning in developing countries as well as in the legislative and executive offices of the developed ones.

JOHN E. BARDACH

University of Hawaii
Hawaii Institute of Marine Biology
Coconut Island
Kaneohe, Hawaii 96744, USA

(R161)

Economic Impacts of Extended Fisheries Jurisdiction. *Edited by L. G. Anderson. Ann Arbor Science Publications, Inc., Ann Arbor, Mich., 1977. xii + 428 p. $24.50.*

This publication contains 19 papers, the proceedings of a symposium sponsored by the University of Delaware Sea Grant Program and the National Marine Fisheries Service. Despite the propensity of economists (as is the case in most disciplines) to communicate primarily with each other, the book is sufficiently diverse in content to be of interest to anyone involved in fisheries resource management. In this regard, the book contributes a perspective of the international, economic, social, and institutional ramifications of managing the extended fisheries jurisdiction of the United States and Canada. *At this stage* in the development of Canada's commercial fisheries, it is felt that the papers by F. W. Bell, F. T. Christy Jr., G. R. Munro and the coauthored paper by G. Ponticorvo, D. M. Johnston, and M. Wilkinson are particularly appropriate.

Economically "accessible" fisheries in North America have generally been characterized by excessive invest-

ment in fishing effort relative to the productive capacities of the resources. This situation has resulted in depleted fish stocks, depressed returns to labor and capital engaged in exploiting the resource, economically depressed communities, a requirement for perpetual government subsidies, a high tax burden, foregone returns to society in the form of a resource rent, and, in general, the misallocation of resources. The fundamental reasons for these phenomena have, in large measure, been attributed to the management of fisheries resources as common property and the failure or inability of public management agencies, as stewards of public fisheries resources, to exercise proprietary rights to control fishing effort. This is truly an example of the "tragedy of the commons" (Hardin 1968). It has precipitated economic and social hardship.

Traditional harvest control measures have tended to place restrictions on fishing effort to maintain the biological productivity of fish stocks. Familiar harvest controls include gear restriction, closed seasons, closed areas, and quotas. Experimentation with restricting the number of participants engaged in exploiting a fishery has also been undertaken. To the extent that such controls restrict destructive fishing and maintain the productivity of fish stocks, they may be judged as effective. However, none of these controls have contributed greatly to the economic value of the resource to the fishing industry or to the general public. They are insufficient conditions to manage fisheries resources. They have failed to control overcapitalization in the industry and, as a result, they have failed to control excessive fishing effort.

The economic solution to the problem of controlling fishing effort, consistent with the productive potential of fisheries resources, which appears to be favored by a number of economists who are working in fisheries resource management, requires the implementation of a pricing system in conjunction with restricted entry. Historically, a major input into the fishing industry, the fish, has generally been priced at zero. This situation, coupled with ease of entry into the industry, has resulted in the erosion of profit margins and the pervasive tendency for the cost of production to exceed the value of production. As a result, the industry has suffered and society has not received a return from public resources in the form of a resource rent. Thus, although the North American taxpayer incurs the cost of management, there is no commensurate return.

Restricted entry, related to investments in fishing effort required to exploit the productive capacity of economically accessible fisheries, provides a means of controlling the number of participants in a fishery. It is not, however, a sufficient control. It will not provide a long-term means of controlling the erosion of profit margins, of permitting a return to labor and capital engaged in the industry, or of permitting a return to the resource. Experience with the British Columbia salmon fishery substantiates this claim. Despite a program of restricted entry and a reduction in the size of the salmon fleet through an expensive "buy-back" program, there has actually been an expansion in investments in fishing effort and a resultant expansion in the productive capacity of the industry. The program was an initial success in terms of increased returns to the residual fleet. The industry obtained "super" profits which included the value of the resource, the resource rent. However, two predictable phenomena occurred and the super profits, which emerged as a result of the reduction in the size of the fleet, were again in a position to be dissipated. First, the super profits became capitalized into the assets of individual licenses and were captured by the original owners who chose to sell their enterprises. In this case, the super profits did not accrue to the subsequent license owner but were effectively dissipated. Second, an incentive was created for individual enterprises to invest in larger, more productive vessels in the interest of capturing a larger share of the harvest. This situation again led to overinvestment in the industry and the pervasive tendency to dissipate profits. In addition, there was no direct return to the resource "stockholders," i.e. the taxpayers who bear the tremendous costs of management.

Although the economic solution to this problem has been articulated for over two decades, for over two decades the contribution of economics to fisheries management has been largely ignored. Essentially, the solution requires the initiation of a price system to allocate scarce fisheries resources. Such a system could be implemented through the competitive sale of licenses or through a royalty on production. By charging a price for publicly owned fish, investments in fishing effort would reach an equilibrium at a lower level of aggregate production than that which would occur when fish are priced at zero. The price could be set sufficiently high to extract all of the rent, or a portion of the rent could be left to the industry. Regardless, society at large would obtain a direct return and the aggregate level of fishing effort could be controlled at levels consistent with the productive capacity of the resource. Although a pricing system may be regarded as a radical departure from traditional fisheries management, it is not a new concept. Pricing systems are used to allocate most other public resources (although perhaps not used effectively). Obviously, it has always been the basis for allocating resources in the private sector of North American society. Nevertheless, a fundamental change is required in past fisheries management practices.

The extension of fisheries jurisdictions in Canada and the United States to 200 miles provides an opportunity for the respective governments to exercise proprietary rights over coastal fisheries resources and control the tragedy of the commons. How well we will succeed will depend on how well we have learned our lessons. Will our coastal fisheries be managed to enhance the welfare of all society, or will they become an even greater liability? F. W. Bell feels "dismayed" at the likely results for the extension of the United States jurisdiction. In his paper "World-Wide Economic Aspects of Extended Fisheries Jurisdiction Management," Bell implies that the extended jurisdiction is likely to be an extended liability. Economic ignorance and a failure "to promote the highest efficiency in the use of vessels and fishermen as is our national purpose in every sector of our economy" have contributed to the current fisheries problems. Bell explains that an overriding concern with the conservation of fish and an inability "of coming to grips" with the ramification of managing fisheries resources as common property have led to management schemes of "quotas and regulated inefficiency" which have had "very limited success in preventing the fisheries resource from depletion." Bell feels that there is a likelihood that traditional harvest control measures (e.g. quotas) will continue to be used in the management of the extended jurisdiction with little concern for the economic consequences of these measures. As a result, the extended jurisdiction will not solve the fundamental problem of managing fisheries resources as common property, but will

perpetuate the present tendency of overcapitalization and the need for government assistance.

F. T. Christy, in his paper "Limited Access Systems Under the Fishery Conservation and Management Act of 1976," largely substantiates the concerns of Bell. Christy observes that the Fisheries Conservation and Management Act of 1976 (Public Law 94-265), extending U.S. fisheries jurisdiction to 200 nautical miles "... is detrimental to the taxpayer, to society as a whole and, eventually, to the fishing industry as well." The central concern of Christy is not only the failure of the act to consider a pricing system as a necessary condition to manage fisheries resources, but also the actual prohibition against a pricing system for the domestic industry. As a consequence, a necessary economic condition to control fishing effort and to extract a resource rent is effectively eliminated. This problem will be compounded if resource management agencies fail to initiate a limited access system on the assumption the extension of jurisdiction will eliminate current problems of excessive investment and that a limited access system is therefore not required. Christy explains that such an assumption "will create serious difficulties for fisheries management." As such, if the implications of limited access systems are postponed "... we will then be faced by an enormous amount of superfluous capital and labour — not simply the amount presently engaged but also all the newcomers attracted by promises of new resources and perhaps, unhappily, by subsidy programs as well."

The implications of the United States experience are exceedingly important in Canada, not only for the extended jurisdiction, but for existing coastal and inland fisheries. G. R. Munro notes in his paper "Canada and Fisheries Management with Extended Jurisdiction: A Preliminary View," that, although the Canadian fishing industry represents a rather minor component of gross national product and makes a similar contribution to employment, fisheries resources are of considerable importance to regional economies. As such, the exercise of property rights over fisheries resources within Canada's extended jurisdiction will be of critical importance, particularly on the Atlantic coast. Canada's current interest in asserting "sovereign rights" with respect to the exploitation of fisheries resources enhances the opportunity of a "rational, efficient management system" to control fishing effort. However, given Canada's experience in controlling fishing effort through entry limitation, as in the case of its west coast salmon fishery, a concern is registered whether the benefits of a national management system will exceed or be exceeded by the cost of management. A major problem confronting Canada in the management of its extended jurisdiction concerns not only the exercise of proprietary rights in the control of foreign fishing interest, but also the effective control of its domestic fishing fleets with respect to fishing effort and the generation of a resource rent. Failure to understand the economic ramifications associated with controlling fishing effort and maximizing the national benefit to be derived from the fisheries can readily result in the misallocation of resources.

The paper entitled "Conditions for Effective Fisheries Management in the Northwest Atlantic," coauthored by G. Pontecorvo, D. M. Johnston, and M. Wilkinson, provides a perspective for an efficient management system including the requirements for limited entry and a taxation system. It is noted that the objective of regulation under extended jurisdiction to ensure efficient utilization of resources involves a concern not only for fish stocks, but also for labor and capital engaged in the fisheries. In this regard, efficient utilization of resources requires that a transfer of capital and labor out of the fishing industry, which would increase the value of output of another industry, would not decrease the value of the output of fish. According to this definition, it would appear that there are very few efficiently managed fisheries in Canada. As a matter of fact, it might be argued that a transfer of labor and capital out of the fisheries of Canada might actually increase the value of production. What is more interesting still, a major objective of fisheries management appears to be the generation of employment opportunities (or perhaps disguised unemployment) in an industry that is notorious for excess capital and labor.

The extension of fisheries management jurisdiction to a 200-mile zone provides an opportunity to realize net economic benefits to Canada and the United States and to mitigate the ever present social problems associated with fisheries exploitation. For many economists, the successful management of the extended jurisdiction requires the adoption of economic efficiency criteria to obtain a proper deployment of resources. To ignore this warning can readily result in excessive fishing effort and the perpetuation of economic and social hardship. In providing a commentary, Crutchfield observed, "Perhaps most important in the context of the extended jurisdiction is that it is vastly easier to prevent excess effort from developing than to unscramble the eggs after it has developed."

DENNIS M. CAUVIN

Department of Fisheries and the Environment
Fisheries and Marine Service, Western Region
Winnipeg, Man. R3T 2N6

(R162)

HARDIN, G. 1968. The tragedy of the commons. Science 162: 1243–1248.

Proceedings of the First International Conference on Aquaculture Nutrition. *Edited by Kent S. Price Jr., William N. Shaw, and Karin S. Danberg. College of Marine Studies, University of Delaware, Newark, Del., 1976. vii + 323 p. $3.00.*

The First International Conference on Aquaculture Nutrition was held in Lewes/Rehoboth, Delaware, 1975, and was sponsored by the Sea Grant College Program at the University of Delaware in cooperation with the United States/Japan Aquaculture Panel. The purpose of the conference and publication of the proceedings was to facilitate a better understanding of aquaculture nutrition, a pressing problem area in the utilization of aquatic resources for food production.

This book consists of well-written papers with useful references on general nutrition and fish, crustacean, and molluscan nutrition studies presented by scientists from the United Kingdom, Japan, and the United States, where most of the work in this area has been conducted. In addition, the book contains a suitable summary of papers, table of contents, index of scientific names of all organisms

considered, and a list of speakers and attendees with addresses.

In essence, the book provides a useful overview of the studies in aquaculture nutrition, including nutritional requirements and feed development and culture of organisms. It gives equal emphasis to the nutrition of fish, crustaceans, and molluscs. It includes papers on salmonids, warmwater fish (channel catfish, carp, eel) and red sea bream nutrition, yellowtail feed research, and tropical fish and crustacean food sources. There are papers on the protein and amino acid requirements of *Macrobrachium* species (Asian prawn) larvae, on factors involved in development of feeds for prawns, on culture and feeding of penaeid shrimp indicating the relationship between their maturation stages and food most suitable for each stage, on the nutrition of forage crustaceans (*Moina*, *Artemia*, *Daphnia*), and on lobster nutrition. There are five papers dealing with molluscs (oysters, clams, mussels, abalone, scallops). They are on the use of algal (species listed) and nonalgal diets for intensive culture of molluscs, on the potential sources of food, both soluble and particulate, for mollusc larvae, on the mass culture and feeding of mollusc larvae, and on the feeding and techniques of culturing abalone. A review of the studies at the University of Delaware on the development of a prototype system for the production of molluscs by intensive culture is presented, along with a list of some important research and development activities that should be pursued. The role of the feed industry and significance of basic and applied nutrition to the development of formulated feeds for aquaculture was also considered.

The summary statement of the papers presented pointed out the elements common to the problems of aquaculture nutrition. They are the definition of nutritional requirements and then the creation or finding of food needed by the organisms being cultured. It emphasized the importance of aquatic medium (environment) to nutrition, differences between nutrition and feed research, the importance of standards and standard procedures for comparison of research results, the potential of natural foods, problems of scale in reference to the feed industry and algal production, and the need for specific foods for specific organisms. It gives us some gems of wisdom with near-universal applicability which we should remember in growing any species. Some of these include: nutrient leaching from feeds is a major impediment to definition of nutrient requirements and hence feed development; healthy parents produce healthy progeny; nutrition plays a vital role in maturation of species; and generally nutrition and disease are related. From reading the papers and summary, it becomes obvious that there is a lack of knowledge about the nutrition, feeds, and culture of organisms presently being considered, and this is primarily attributed to the lack of strong, long-range funding commitments. Meanwhile, it was suggested we must continue to develop feeds for organisms by using a combination of empirical and fundamental (using available basic nutritional and physiological information) approaches, but the empirical approach should be limited.

This book should be of interest to research managers and scientists, professors, students, and others in aquaculture and related or relevant areas such as biology, biochemistry, and toxicology. The references after each paper will facilitate one's obtaining additional, more detailed or more comprehensive information of interest. The book contains considerable valuable information and should be a required reading text for more advanced students in aquacultural and nutritional sciences. It is available at a nominal cost that all institutional libraries and individuals interested in aquaculture nutrition should be able to afford.

M. YURKOWSKI

Department of Fisheries and the Environment
Fisheries and Marine Service
Freshwater Institute
Winnipeg, Man. R3T 2N6 (R142)

Inland Fishes of California. *Peter B. Moyle. University of California Press, Berkeley and Los Angeles, California, 1976. viii + 405 p. $20.00.*

Books that deal with California's unique flora and fauna invariably open with a general statement about California's multitude of habitats and its diverse array of species. Thankfully, this book does not, but it could very well open with a statement about how interest in a book about the fishes of California may stem from the diverse "habits" of Californians; that is, fisheries biologists, anglers, conservationists, environmental consultants, and numerous other specialists have particular areas of interest that they would expect to be covered in a book on California fishes. Dr Moyle has attempted to provide a text with a broad enough coverage that will satisfy all these interests. He has succeeded in this task and I believe that this book will be very well received by each of these specialty groups.

In a unique introductory format that is unlike any previous faunal study that I have seen, the author has devoted chapters to the ecological features of several California drainage systems (22 pages) and to the changes that have occurred in the composition and abundance of the inland fish fauna of California, including planned and accidental introductions (13 pages). These two sections complement the chapter on distribution and zoogeography (20 pages), which is largely a summary of the work of Drs R. R. Miller and C. L. Hubbs. Brief sections on fish identification (7 pages) and structure (2 pages) will also be of interest to anglers and budding ichthyologists.

In addition to family, generic, and specific keys and a distributional checklist of species by major drainage system, each of the California species is illustrated and treated individually. These species descriptions include paragraphs on identification, origin of common and scientific names, distribution, status (in terms of past, current, and projected changes in distribution, population size, and exploitation by both anglers and commercial fisheries), a summary of information on life history aspects, and selected references. No references are later than 1974 and the inclusion of distributional records for 1975 as footnotes suggests a rather long delay between the time the text was finished and the actual publication date (Fall 1976).

The majority of the illustrations in the book are very good, although a few lack detail. Similarly, while the book is generally well referenced, certain life history sections could have included additional citations. Most of the information presented in these sections is a summary of other workers' contributions rather than those of the author (e.g. about one third of the references are California Fish and Game publications). However, with regard to this last point, the author should be commended on his ability to

combine and synthesize a large amount of detailed information in the relatively short time that he has studied California fishes. A list of corrections and additions to the text has been prepared by Dr Moyle and is available from him on request. The minor shortcomings mentioned above do not significantly limit the usefulness of this work. Undoubtedly a revised edition will include updates on many of the research problems proposed in the text and currently under investigation by the fisheries group at the University of California at Davis and other workers in California.

Dr Moyle's writing style is quite enjoyable and the sprinkling of humorous comments throughout the text add to its readability. The text is conservation oriented and some of the approaches suggested for complex environmental problems may seem controversial to readers with divergent (or vested) interests. However, all things considered, this book will be a valuable asset to everyone with interest in California fishes, from the professional fisheries biologist to the weekend angler (not necessarily mutually exclusive categories). Similarly, the moderate cost for a university press publication ($20) should also add to its wide circulation. In summary, the "Inland Fishes of California" certainly goes against the old adage of not being able to be "all things to all people," and is a welcome addition to our state's collection of faunal studies.

VINCENT H. RESH
Division of Entomology and Parasitology
College of Natural Resources
University of California
Berkeley, California 94720, USA (R141)

Fishes of the World. *Joseph S. Nelson. John Wiley and Sons, Inc., New York, N.Y., 1976. xiii + 416 p., many figures, 45 maps. $26.90.*

This book deals with the higher classification of living and fossil fishes, usually from family level upwards (although examples of genera are given, and the hierarchy sometimes descends to tribal categories). Its aim is to present "a modern introductory systematic treatment of all major fish groups" to serve as a "text for fish systematic courses, and a reference for professional workers." Nelson breaks down the fishes into 6 classes, 4 of which are extant and are comprised of 46 orders and 450 families. Treatment of the families is highly variable, depending on the amount of information available to Nelson (p. iv). For example, the extinct suborder Brachythoracoidei is said to consist of 14 families (of which only 3 are named), but the Blenniidae is broken down to 2 subfamilies made up of 5 tribes (all of which are described). In most cases a short description (which may or may not be diagnostic) is offered, together with some 430 outline drawings of family representatives. Maps show the geographical distribution of certain families.

The book is basically a review of developments up to 1973 in the higher classification of fishes. The approach to classification taken by Nelson "largely" favors the classical methods of Mayr (gradism), which has not made the author's task any easier (since most of the recent studies on fish higher classification have been genealogical). The result is something of a potpourri, with bits taken from gradistic authors intermingled with a generally broad acceptance of classifications proposed by "phylogenetic" authors (phylogeny here defined in the Hennigian, rather than Mayrian, sense — a point not clarified by Nelson in his use of the term). One somewhat disturbing factor is that Nelson accepts many of the cladistic proposals on fish classification put forward in the osteichthyan section of the multiauthored "Interrelationships of Fishes" (1973), yet rejects Campagno's suggestions for the elasmobranchs. This may be covered by Nelson's statement of "... not prematurely accepting some new, unorthodox view of phylogeny before it has been "tested" (his quotes) and has gained some acceptance." (p. viii–ix), but then it is difficult to comprehend why this did not apply to a number of other authors in the same volume whose conclusions he did accept. Certainly there is a source of confusion (in terms of inconsistency) both for the student and for the professional unfamiliar with the group. Perhaps a more perturbing point may be illustrated by the same example (although there are other such examples in the text). In discussing Campagno's classification, he states it is "a split classification in which 49 families compare with the 21 I recognize." (p. 29). Nelson presents no evidence why he recognizes 21 families, whether he in fact has any information on the topic, whether he is following any previous classification, or whether he is juggling previous works and presenting us with a new arrangement. Statements of this nature are highly confusing. (This reviewer is not competent to comment on how many families of elasmobranchs it is useful to recognize, but is disturbed by unsubstantiated, and thus apparently arbitrary, statements such as this).

There are, of course, certain differences between this reviewer and Nelson on the philosophical "raison d'être" of classification, and, because of these differences, I would not agree that fossils are essential to construction of hypotheses of relationship, nor that it is necessary that there be "major disagreements" in our future classifications. Extensions of these philosophical differences reach into Nelson's classification itself (for example, his separation of the Syngnathiformes from the Gasterosteiformes, a group that should probably include the Indostomiformes as well), but since Nelson has more or less stated his alignment with the gradists, these criticisms are secondary. There are several other minor areas where I do not feel that Nelson has given the matter a great deal of reflection, e.g. "No classification to date can claim to present the final truth." (p. 10). Classification (whether phenetic, gradistic, or phylogenetic) can only be an hypothesis, and as such is logically incapable of presenting "the final truth."

There are a number of systematic errors and inconsistencies at the alpha level in the book, for example, *Terapon* not *Therapon* (p. 224–225), and there is but one species of *Zanclus* (not two p. 283). Other "errors" were probably not so at the time the book went to press, but should be changed in any future edition; e.g. it is doubtful whether *Rabula* is distinct from *Gymnothorax* (p. 86); *Pseudocrenilabrus natalensis* is not "possibly" a grammid, but is a cichlid (p. 223); the most widely introduced cichlid is no longer a *Tilapia* but a *Sarotherodon* (p. 251). *Acropoma* is listed as a member of the Percichthyidae, yet we are told at the end of that list that it "is retained in a separate family here" (p. 220). Glaucosomids are credited with a lunate caudal fin, although the fish figured has a suspiciously truncate caudal (p. 224).

At a higher level, it is somewhat surprising to find that Nelson retains (albeit with some reservations) the families Kasidoroidae and Rosauridae, when the former has been shown to be a gibberichthyid and the latter a giganturid.

Anatomical errors arise partly through the difficulty of diagnosing or generalizing about any one family in a precise way, but this has led to numerous inaccurate statements, e.g. pelvic fins are absent in more than one carangid, and *Parastromateus niger* lacks them at sizes greater than about 5 cm (p. 233); in the pomacentrids, some species of *Chromis* and all members of *Dascyllus* have two nostrils, and many plankton-pickers (ca. 50 spp) have a terete body form — neither condition can really be called "rare" (p. 251); the acanthurid *Naso* (= *Axinurus*) *thynnoides* is not a herbivore (p. 282); two monotypic genera of tetraodontiforms possess pleural ribs (p. 301).

More trenchant anatomical errors include: dactyloscopids are not "unique to other teleosts" in possessing a branchiostegal respiratory pump, which is found (presumably convergently) in all tetraodontids and diodontids (p. 266); the high-headed appearance of acanthurids surely has more to do with the elongated ethmoid than with the elongated nasals. Particularly confusing and inconsistent is Nelson's terminology for the series of bones encircling the lower half of the orbit. Although there is no universally applied name for these bones, most authors are at least consistent in the name they choose to use. A brief survey revealed the following names used for parts or all of this series of homologous ossifications: circumorbitals (p. 194, 198), lachrymal (p. 194, 198, 201), suborbital (p. 200, 226), and preorbital (p. 204, 205).

Odd expressions include "McDowell (1973) and Templemen (1973) each describe nine specimens collected since the holotype (collected in 1887), but all are different specimens." (p. 93). Since Nelson recognizes only one species, the last word of the quote presumably cannot be an error for "species." Liem "apparently agrees with Barlow et al. (1968) that..." (p. 248), which is scarcely surprising since Liem is one of the "et al.". Typographical errors appear to be nonexistent, which is refreshing in a book of this nature.

In summary, this book will, in the majority of cases, provide the user with a rapid index to the families of fishes recognized by Nelson, and a reference to some of the more modern literature prior to 1974. It will usually provide some idea of the family through line drawings and brief descriptions. It does represent the most up-to-date collation of the literature available (the English translation of Lindberg, published in 1974, notwithstanding — a book, incidentally, which to confuse matters has the hard-cover title of "Fishes of the World," and which is also produced by John Wiley and Sons). It will be useful for the casual interests of the professional and the not so casual interests of the student. However, this reviewer is of the opinion that the publishers have priced the book out of the latter market.

It is an extremely unfortunate circumstance that in the last 3 years or so since Nelson submitted the manuscript, a tremendous volume of literature has been published on aspects of the higher classification of fishes. Recent advances are appearing so rapidly that any book of this nature is inevitably out of date by the time the publisher can produce it.

RICHARD WINTERBOTTOM

Department of Ichthyology and Herpetology
Royal Ontario Museum
100 Queen's Park
Toronto, Ont. (R136)

Books received/Livres reçus

June 1977

Grassy Narrows. *George Hutchison and Dick Wallace. Van Nostrand Reinhold Ltd., Scarborough, Ontario, 1977. xiv + 178 p. $8.95.* (A photojournalistic account of the Grassy Narrows Indian Reserve in Northwestern Ontario, and the peoples' responses to modern stress, particularly mercury contamination of one of their food resources.)

No Safe Place. *Warner Troyer. Clarke, Irwin and Co., Ltd. Toronto, Ontario, 1977. xvi + 267 p. $13.95.* (The body of this book deals with mercury pollution in the Grassy Narrows and White Dog Indian Reserve areas of the English-Wabigoon river system of Northwestern Ontario. In addition, there is some coverage of other dangerous pollution levels in other parts of the world.)

Fishwatchers' Guide to the Inshore Fishes of the Pacific Coast. *Daniel W. Gotshall. Sea Challengers, Monterey, California, 1977. 112 p.* (A beautifully illustrated short guide aimed at the intelligent fish equivalent of birdwatchers.)

Laboratory Exercises in Oceanography. (With Teacher's Manual). *Bernard W. Pipkin, Donn S. Gorsline, Richard E. Casey, and Douglas E. Hammond. W. H. Freeman and Co., San Francisco, California, 1977. xii + 225 p. $6.95. (66 p. in Manual).* (A very elementary first course in oceanography designed for students in general first or second year Science or Arts.)

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RECENT PUBLICATIONS / RÉCENTES PUBLICATIONS

The number following each title in each series refers to the establishments listed at the end of the section.

Les nombres qui suivent les titres de chacune des séries désignent les établissements suivants à la fin de la section.

Recent Studies

Until 1970, reprints of these articles had been included in an annual volume of "Studies," composed of two parts. The final binding was the 1969 Studies, Part 2, which included No. 1355. These are no longer bound and distributed. We continue, however, to number and list all articles on investigations published in other periodicals, which henceforth may be obtained in reprint form only from the author or originating establishment.

2382. HECKY, R. E. 1977. The use of diatom microfossils in interpreting the distribution of pore water solutes in Small Momela Lake (Tanzania), p. 197–202. *In* Interactions between sediments and fresh water: Proc. Int. Symp. Dr. W. Junk, B. V. Publishing, The Hague. (4)

2383. SCHINDLER, D. W., R. HESSLEIN, AND G. KIPPHUT. 1977. Interactions between sediments and overlying waters in an experimentally eutrophied Precambrian Shield lake, p. 235–243. *In* Interactions between sediments and fresh water: Proc. Int. Symp. Dr. W. Junk, V. V. Publishing, The Hague. (4)

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2393. MITCHELL, E. D. 1975. Prelinary report on Nova Scotia fishery for sperm whales (*Physter catodon*), p. 226–235. *In* Int. Comm. Whaling, 25th Rep. Comm., London. (5)

2394. MITCHELL, E. D., AND V. M. KOZICKI. 1975. Prototype visual mark for large whales modified from "Discovery" tag, p. 236–239. *In* Int. Comm. Whaling, 25th Rep. Comm., London. (5)

2395. MITCHELL, E. D. 1975. Progress report on whale research, May 1973–May 1974, p. 270–282. *In* Int. Comm. Whaling, 25th Rep. Comm., London. (5)

2396. MITCHELL, E. D. 1975. Preliminary report on Nova Scotia fishery for sei whales (*Balaenoptera borealis*), p. 218–225. *In* Int. Comm. Whaling, 25th Rep. Comm., London. (5)

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2400. KOZICKI, V. M., AND E. D. MITCHELL. 1974. Permanent and selective chemical marking of Mysticete ear plug lamination with quinacrine, p. 142–149. *In* Int. Comm. Whaling, 24th Rep. Comm., London. (5)

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Jusqu'en 1970, ces articles étaient réimprimés, puis reliés dans un volume annuel d'études, comprenant deux parties. Les études de 1969, partie 2, incluant le n° 1355, ont été les dernières à être reliées. Nous n'en faisons désormais plus la reliure ni la distribution. Nous continuons cependant de numéroter les articles et d'en établir des listes d'études sur des recherches mentionnées dans d'autres périodiques. On peut donc se les procurer, sous leur forme réimprimée seulement, de l'auteur ou du service dépositaire.

Translation Series

The following translations have been prepared by or for the Fisheries and Marine Service, for use in its investigations. Copies are available from Translation Services, Canada Institute for Scientific and Technical Information, National Research Council of Canada, Ottawa, Ontario K1A 0S2, at a cost of 22¢ per page and a minimum charge of $2.20. Information on translations can be obtained from the Scientific Information and Publications Branch.

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Interpretive Articles Series

This new series commenced in 1966. The articles interpret work already published in primary journals. They appear at irregular intervals in various technical publications. Frequently an article essentially duplicates, condenses, or is based on an article in another series.

368. ADDISON, R. F. 1975. Review of "The chemistry of PCB's" by O. Hutzinger, S. Safe and V. Zitko (CRC Press, 1974). Sci. Total Environ. 2 p.

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Cette série a débuté en 1966. Les articles donnent une explication de travaux déjà publiés dans des revues prioritaires. Ils paraissent à intervalles irréguliers, dans diverses publications techniques. Souvent, un article se basera sur un écrit d'une autre série, le condensera ou le reproduira presque tel quel.

369.(F) MITCHELL, E. 1973. Les baleines dans le monde. Nat. Can. 2: 1–21. (5)

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This series includes unpublished preliminary reports and data records not intended for general distribution. They should not be referred to in publications without clearance from the issuing establishment and without clear indication of their manuscript status.

1420. WESTRHEIM, S. J. 1977. Length–weight and length–girth relationships, maturity, spawning season and diet of Pacific cod (*Gadus macrocephalus*) collected in British Columbia waters during April 1975–February 1976. Fish. Mar. Serv. MS Rep. 1420: 68 p. (1)

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Rapports manuscrits

La série comprend des articles d'information et des rapports préliminaires non publiés, qui ne sont pas destinés à la distribution générale. Ils ne doivent pas être donnés en références sans l'assentiment du service dépositaire et sans une indication claire de leur forme manuscrite.

1422. BIGG, M. A., I. B. MACASKI, AND G. ELLIS. 1977. Studies on captive fur seals, progress report no. 1. Fish. Mar. Serv. MS Rep. 1422: 23 p. (1)

1423. KETCHEN, K. S. 1977. A summary of foreign and domestic fisheries for groundfish off the west coast of Canada, 1964–1975. Fish. Mar. Serv. MS Rep. 1423: 35 p. (1)

List of Establishments

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Fisheries and Marine Service
Pacific Biological Station
P.O. Drawer 100
Nanaimo, British Columbia V9R 5K6

(2) Department of Fisheries and the Environment
Fisheries and Marine Service
Vancouver Laboratory
6640 N.W. Marine Drive
Vancouver, British Columbia V6T 1X2

(3) Department of Fisheries and the Environment
Fisheries and Marine Service
Pacific Environment Institute
4160 Marine Drive
West Vancouver, British Columbia V7V 1N6

(4) Department of Fisheries and the Environment
Fisheries and Marine Service
Freshwater Institute
501 University Crescent
Winnipeg, Manitoba R3T 2N6

(5) Department of Fisheries and the Environment
Fisheries and Marine Service
Arctic Biological Station
P.O. Box 400
Ste. Anne de Bellevue, Quebec H9X 3L6

(6) Department of Fisheries and the Environment
Fisheries and Marine Service
Biological Station
St. Andrews, New Brunswick E0G 2X0

(7) Department of Fisheries and the Environment
Fisheries and Marine Service
Marine Ecology Laboratory
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(10) Department of Fisheries and the Environment
Fisheries and Marine Service
Scientific Information and Publications Branch
116 Lisgar Street
Ottawa, Ontario K1A 0H3

(11) Department of Fisheries and the Environment
Fisheries and Marine Service
Canada Centre for Inland Waters
Great Lakes Biolimnology Laboratory
P.O. Box 5050
867 Lakeshore Rd.
Burlington, Ontario L7R 4A6

Liste d'établissements

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Service des pêches et de la mer
Station biologique du Pacifique
C.P. 100
Nanaïmo (Colombie-Britannique) V9R 5K6

(2) Ministère des Pêches et de l'Environnement
Service des pêches et de la mer
Laboratoire de Vancouver
6640 nord-ouest, prom. Marine
Vancouver (Colombie-Britannique) V6T 1X2

(3) Ministère des Pêches et de l'Environnement
Service des pêches et de la mer
Institut de l'environnement du Pacifique
4160, prom. Marine
Vancouver-Ouest (Colombie-Britannique)
V7V 1N6

(4) Ministère des Pêches et de l'Environnement
Service des pêches et de la mer
Institut des eaux douces
501, University Crescent
Winnipeg (Manitoba) R3T 2N6

(5) Ministère des Pêches et de l'Environnement
Service des pêches et de la mer
Station biologique de l'Arctique
C.P. 400
Saint-Anne-de-Bellevue (Québec) H9X 3L6

(6) Ministère des Pêches et de l'Environnement
Service des pêches et de la mer
Station biologique
St. Andrews (Nouveau-Brunswick) E0G 2X0

(7) Ministère des Pêches et de l'Environnement
Service des pêches et de la mer
Laboratoire d'écologie marine
Institut de Bedford C.P. 1006
Dartmouth (Nouvelle-Ecosse) B2Y 4A2

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Bibliothèque de la région des maritimes
C.P. 550
Halifax (Nouvelle-Ecosse) B3J 2S7

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Service des pêches et de la mer
Services des recherches et des ressources
Région de Terre Neuve
3, rue Water
St-Jean (Terre-Neuve) A1C 1A1

(10) Ministère des Pêches et de l'Environnement
Service des pêches et de la mer
Direction de l'information et des publications scientifiques
116, rue Lisgar
Ottawa (Ontario) K1A 0H3

(11) Ministère des Pêches et de l'Environnement
Service des pêches et de la mer
Centre canadien des eaux intérieures
Laboratoire de biolimnologie des Grands Lacs
C.P. 5050
867, ch. Lakeshore
Burlington (Ontario) L7R 4A6

Call for Papers

12th Congress of the Canadian Meteorological and Oceanographic Society

May–June 1978
London, Ontario

The twelfth Annual Congress and Annual General Meeting of the Canadian Meteorological and Oceanographic Society will be held at the University of Western Ontario, London, Ontario, at the end of May 1978. The theme of the opening session will be "Energy, the Meteorologist and the Oceanographer" as presented by invited and contributed papers. Subsequent sessions will deal with contributed papers on meteorology and oceanography, including sessions of common interest, according to the papers submitted.

Titles and definitive abstracts (less than 300 words) should reach the program committee by *February 1 1978*. Papers on meteorology should be sent to Dr D. R. Hay, Department of Physics, University of Western Ontario, London, Ontario, N6A 3K7. Papers on oceanography should be sent to Mr Farrell M. Boyce, Canada Centre for Inland Waters, 867 Lakeshore Road, Burlington, Ontario, L7R 4A6.

Appel d'articles

12^{e} Congrès de la Société canadienne de météorologie et d'océanographie

mai–juin 1978
London, Ontario

Le 12^{e} congrès annuel et assemblée générale de la Société canadienne de météorologie et d'océanographie aura lieu à l'Université Western Ontario, London, Ontario, fin mai 1978. La séance d'ouverture aura pour thème: «L'Energie, la météorologiste de l'océanographe», que traiteront des travaux présentés sur invitation et des contributions qui seront soumises. Les séances suivantes seront consacrées à des contributions sur la météorologie et l'océanographie, y compris séances d'intérêt commun, selon les contributions reçues.

On devra faire parvenir les titres et résumés définitifs (ne dépassant pas 300 mots) des articles au comité du programme avant le *1er février 1978*. Les articles portant sur la météorologie devront être envoyés à M. D. R. Hay, Département de physique, Université Western Ontario, London, Ontario, N6A 3K7. Les articles portant sur l'océanographie devront être envoyés à M. Farrel M. Boyce, Centre canadien des eaux intérieures, 867 Lakeshore Road, Burlington, Ontario, L7R 4A6.

Dickson, and E. E. Herricks) **E. J. Fee**; Herbicides: Chemistry, degradation and mode of action (Edited by P. C. Kearney and D. D. Kaufman) **G. R. B. Webster**; Farming the edge of the sea (E. S. Iversen) **J. E. Bardach**; Economic impacts of extended fisheries jurisdiction (L. G. Anderson) **D. M. Cauvin**; Proceedings of the First International Conference on Aquaculture Nutrition (Edited by K. S. Price Jr., W. N. Shaw, and K. S. Danberg) **M. Yurkowski**; Inland fishes of California (P. M. Moyle) **V. H. Resh**; Fishes of the world (J. S. Nelson) **R. Winterbottom** 2425–2432

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